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KITTREDGE, J. S., FRANCIS T. TAKAHASHI, JAMES LINDSEY, and REUBEN LASKER. Chemical signals in the sea: Marine allelochemics and evolution 1

FULLENBAUM, RICHARD F., and FREDERICK W. BELL. A simple bioeconomic fishery management model: A case study of the American lobster fishery 13

OLLA, BORI L., ALLEN J. BEJDA, and A. DALE MARTIN. Daily activity, movements, feeding, and seasonal occurrence in the tautog, *Tautoga onitis* 27

LENARZ, W. H., W. W. FOX, JR., G. T. SAKAGAWA, and B. J. ROTHSCHILD. An examination of the yield per recruit basis for a minimum size regulation for Atlantic yellowfin tuna, *Thunnus albacares* 37

FLEMINGER, A., and K. HULSEMANN. Systematics and distribution of the four sibling species comprising the genus *Pontellina* Dana (Copepoda, Calanoida) 63

HUGHES, STEVEN E. Stock composition, growth, mortality, and availability of Pacific saury, *Cololabis saira*, of the northeastern Pacific Ocean 121

ANAS, RAYMOND E. Heavy metals in the northern fur seal, *Callorhinus ursinus*, and harbor seal, *Phoca vitulina richardi* 133

WAHLE, ROY J., ROBERT R. VREELAND, and ROBERT H. LANDER. Bioeconomic contribution of Columbia River hatchery coho salmon, 1965 and 1966 broods, to the Pacific salmon fisheries 139

POWELL, GUY C., KENNETH E. JAMES, and CHARLES L. HURD. Ability of male king crab, *Paralithodes camtschatica*, to mate repeatedly, Kodiak, Alaska, 1973. 171

WICKHAM, DONALD A., and GARY M. RUSSELL. An evaluation of mid-water artificial structures for attracting coastal pelagic fishes 181

GRANT, GEORGE C. The age composition of striped bass catches in Virginia Rivers, 1967-1971, and a description of the fishery 193

PEARCY, WILLIAM G., and SHARON S. MYERS. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? 201

PARK, TAISOO. Calanoid copepods of the genus *Aetideus* from the Gulf of Mexico .. 215

LIGHTNER, DONALD V. Normal postmortem changes in the brown shrimp, *Penaeus aztecus* 223

STRUHSAKER, PAUL, and ROBERT M. MONCRIEF. *Bothus thompsoni* (Fowler) 1923, a valid species of flatfish (Pisces; Bothidae) from the Hawaiian Islands 237

Note

CABLE, WAYNE D., and WARREN S. LANDERS. Development of eggs and embryos of the surf clam, *Spisula solidissima*, in synthetic seawater 247

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Fishery Bulletin

CONTENTS

Vol. 72, No. 1 **January 1974**

KITTREDGE, J. S., FRANCIS T. TAKAHASHI, JAMES LINDSEY, and REUBEN LASKER. Chemical signals in the sea: Marine allelochemics and evolution 1

FULLENBAUM, RICHARD F., and FREDERICK W. BELL. A simple bioeconomic fishery management model: A case study of the American lobster fishery 13

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ANAS, RAYMOND E. Heavy metals in the northern fur seal, *Callorhinus ursinus*, and harbor seal, *Phoca vitulina richardi* 133

WAHLE, ROY J., ROBERT R. VREELAND, and ROBERT H. LANDER. Bioeconomic contribution of Columbia River hatchery coho salmon, 1965 and 1966 broods, to the Pacific salmon fisheries 139

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PARK, TAISOO. Calanoid copepods of the genus *Aetideus* from the Gulf of Mexico .. 215

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Note

CABLE, WAYNE D., and WARREN S. LANDERS. Development of eggs and embryos of the surf clam, *Spisula solidissima*, in synthetic seawater 247

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CHEMICAL SIGNALS IN THE SEA: MARINE ALLELOCHEMICS AND EVOLUTION[1]

J. S. KITTREDGE,[2] FRANCIS T. TAKAHASHI,[3]
JAMES LINDSEY,[4] AND REUBEN LASKER[5]

ABSTRACT

Observations in chemical ecology suggest the coevolution of "natural products" of plants and the chemoreceptors of herbivorous insects. We have reviewed evidence which suggests that this coevolution extends back to the primordial protistans. Thus, the evolutionary pressure for the development of a chemosensory capability probably derived from the presence of metabolic products in the milieu. These products are considered to have been both cues to the location of prey and "membrane irritants" evolved in the initial phase of chemical protection. Sometime later this chemosensory capability provided several functions in the evolution of metazoans, i.e. the precursors of developmental signals, hormone function, and synaptic transmission.

We consider that most of the extant "natural products" of plants and marine invertebrates are protective allomones. A feature of allomone function that has been termed "antifeedant" or "feeding inhibitor" may represent the "cryptic odors" of Haldane. We provide evidence that the naphthoquinones with a juglone or naphthazarin structure have this activity. Octopus ink has a "cryptic odor" effect on moray eels. Marine Crustacea have, however, evolved an ability to perceive the orthoquinone precursors of the ink, a warning signal.

Evidence for an array of sex pheromones in a crab and a cycloid swimming pattern in a copepod that may enable it to follow a chemical gradient indicate the complexity of behavioral responses to chemical cues.

The earliest form of interaction between organisms was probably by means of chemical agents. This interaction involved both conflict and cooperation and its existence implies detection of these agents. Haldane (1955) first suggested that chemical communication is the most primitive form of communication, orginating with primordial unicellular organisms. He reasons that this primordial protistan communication was a necessary prelude to the evolution of metazoans and thus is a lineal predecessor of synaptic transmission and hormone reception. This early chemical communication may have evolved as an accessory to the active transport mechanism of the cell membrane or as a "membrane sensitivity" to metabolic by-products (Wynne-Edwards, 1962). That a more detailed understanding of transducer physiology is central to further advances in neurobiology has been emphasized by Delbrück (1970). He considers the stimulus-response system represented by chemoreception or synaptic transmission to be homologous.

We wish to examine some of the recent concepts of chemical ecology and to present examples from the marine environment. Studies of chemoreception are providing evidence for the pervasive function of chemical signals in the environment. The "membrane sensitivity" concept of Wynne-Edwards may provide a clue to both the initial evolution of a transducer function and the continuing evolution of receptor sites of greater diversity and specificity. It is evident that this diversity has resulted from a continual interplay of chemical countermeasures and the development of neurosensory and behavioral adaptations to these agents.

ALLELOCHEMICS

At all levels of life we are finding examples of attack, defense, and behavioral response

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based on chemical agents. These interactions and the characterization of the chemical agents involved are the subject of the newly developing field of chemical ecology (Sondheimer and Simeone, 1970). Chemicals that are syntheized and released by one individual of a species to alter the behavior of other members of the species are termed pheromones. These signals range in their function from trail markers and territorial markers through alarm and defense signals to those which control caste structure in social insects and the sex pheromones that are calling signals and aphrodisiacs. Chemicals also have a wide range of interspecific interactions. A substance produced by one organism may influence the behavior of members of other species. A flower scent that enhances pollination is a well-known example. This field of chemical ecology has been termed allelochemics, and the chemical agents have been subdivided on the basis of function into allomones, which give adaptive advantage to the producing organism, and kairomones, which give adaptive advantage to the receiving organism (Whittaker and Feeny, 1971). The allomones include the repellents produced by many plants and animals, suppressants which inhibit competitors (e.g., fungal antibiotics), venoms, inductants (e.g., gall producing agents), and attractants (e.g., chemical lures). The kairomones include attractants (e.g., the scent of a prey), inductants (e.g., the factor that stimulates hyphal loop development in nematode-trapping fungi), danger signals (e.g., predator scents, secondary plant substances indicating toxicity), and stimulants (e.g., hormones that induce growth in the receiving organism).

The diverse natural products, coumarins, quinones, flavonoids, acetylenes, terpenoids, saponins, cardiac glycosides, alkaloids, thiols, and cyanogenic glycosides, which were long considered metabolic waste products, are now recognized to be allelochemic agents. Examination of the function of these natural products provides some insight into their evolution. Some of these compounds are toxic, some are chemical lures, others inhibit the growth of competitive plant species, but the bulk of these compounds probably function as "feeding inhibitors" of herbivores (Gilbert, Baker, and Norris, 1967; Munakata, 1970). The coevolution of butterflies and plants is considered by Ehrlich and Raven (1964). They emphasize the role of reciprocal selective responses during this evolution and conclude that "the plant-herbivore interface may be the major zone of interaction responsible for generating terrestrial organic diversity." The "accidental" evolution of a metabolic sequence resulting in the production of a noxious substance by a plant provided a selective survival advantage in the clone carrying this capability. Decreased predation by herbivores on those individuals containing the highest concentrations of the new substance resulted in genetic selection for increased synthesis and storage of the noxious substance. Such "protected" species experience an explosive increase because of their protection from contemporary phytophagous organisms. The first evolutionary response of the herbivores must have been the development of the capability to detect the compound, i.e. sensitive external chemoreceptors. Later evolutionary events led to the development in some individuals of a tolerance for the noxious substance. The herbivores which developed this tolerance then had access to a large food supply for which there was no competition. The ability to detect the substance then had an altered function, the feeding inhibitor was now a feeding stimulant. The present evidence of the repeated occurrence of this cycle is the existence of tightly coupled herbivorous insects and their host plants, presumably arising through coadaptation.

In 1955 Haldane, in a consideration of chemical communication and visual signals, wondered if cryptic odors had ever evolved. While most of the feeding inhibitors that have evolved are probably irritants, many may be cryptic odors. It is likely that the two activities may only differ in the membrane affected. The term irritant implies membranic sensitivity and, of those membranes of an organism in immediate contact with the environment, the chemosensory membranes are likely the most sensitive to chemical irritation. In an environment in which a major fraction of the information flow is chemical, any agent capable of disrupting the chemosensory organs of a predator would provide an ideal mechanism for "hiding" from that predator. Cryptic odors may be either "negative odors" altering, for protracted periods, the membrane potential of the dendrites and blocking their normal generator potential, or they may be the chemical equivalent of a

"white noise," producing an "uncoded" array of spikes in the chemosensory neurons.

The best description of behavior suggesting a "cryptic odor" in the marine environment is that given by MacGinitie and MacGinitie (1968). The ink of an octopus is considered a "smoke screen"; however, it can also affect the olfactory sense. The MacGinities observed that after a moray eel swam through the ink cloud of an octopus it could no longer "recognize" an octopus. The moray eel apparently requires both visual and olfactory input for this recognition. They state, "We were surprised to find that the real effect of the ink of an octopus is to paralyze the olfactory sense of its enemies." The melanin of the ink is a polymer of oxidized L-DOPA. The polymerization proceeds through three orthoquinones, dopaquinone (6, Figure 1), dopachrome (7), and indole-5, 6-quinone (8). In the biosynthesis of melanin, this oxidation is catalyzed by polyphenyl oxidases; however, heavy metal ions can also catalyze the oxidation, and it can be readily demonstrated that the trace of heavy metal ions in seawater will rapidly convert L-DOPA to melanin. The octopus ink loses its potency with time, a factor that would indicate that the biological activity of the ink is due to the presence of the unstable monomer orthoquinones in the fresh ink (Kittredge, Takahashi, and Lindsey, unpublished data).

The observation of Gilbert et al. (1967) that juglone (5-hydroxy-1,4-naphthoquinone) (1, Figure 1) is a deterrent to feeding by the bark beetle, *Scolytus multistriatus*, suggested a similar function for the polyhydroxynaphthoquinones occurring in the echinoderms. These spinochromes are all derivatives of juglone (1) or naphthazarin (2). They occur as soluble salts in the tissues and may be present in considerable amounts in the larvae. They also occur as insoluble calcium salts in the spines and tests (Thompson, 1971). The echinoids have received the closest attention, but P. J. Scheuer and his group have demonstrated the presence of these compounds in the other four classes of this phylum—the holothurians, asteroids, ophiuroids, and crinoids (Singh, Moore, and Scheuer, 1967). They also demonstrated the presence of a substituted 2,5-benzoquinone (3) in the genus *Echinothrix* (Moore, Singh, and Scheuer, 1966). The crinoids are interesting in that they contain primarily a series of polyhydroxyanthroquinones (e.g., rhodocomatulin,

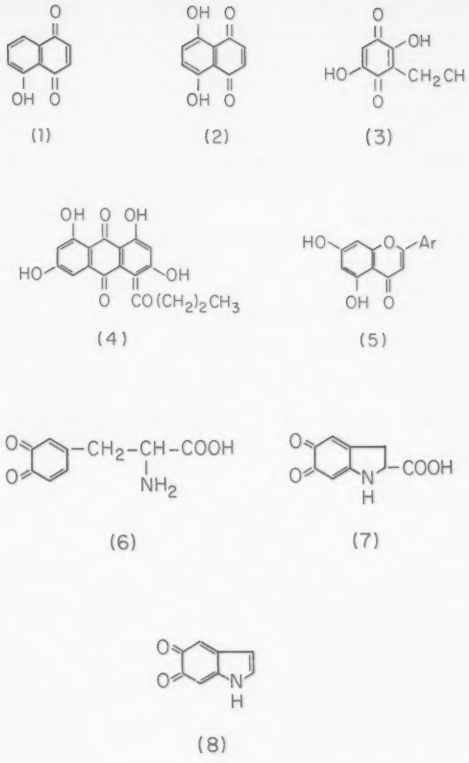

FIGURE 1.—Structures of compounds typical of those which may function as "cryptic odors." (1) juglone, (2) naphthazarin, (3) 2, 5-dihydroxy-3- ethylbenzoquinone, (4) rhodocomatulin, (5) flavone, (6) dopaquinone, (7) dopachrome, (8) indole-5,6-quinone.

4) (Sutherland and Wells, 1967; Powell, Sutherland, and Wells, 1967; Powell and Sutherland, 1967; Matsuno et al., 1972; Erdman and Thomson, 1972).

Utilizing the "feeding response" of the lined shore crab, *Pachygrapsus crassipes*, which consists of a rapid lateral movement of the mouthparts when presented with a feeding stimulus, we have bioassayed the "feeding inhibitor" activity of juglone and eight representative spinochromes. The "feeding stimulus" was a 20-μl aliquot of a 3-mM solution of taurine in seawater administered from a repeating syringe close to one of the antennules of the crab. Initially the crabs were immersed in a 1-μM solution of the naphthoquinone and tested for a feeding response. Five experimental and

one control crab were utilized for each compound. No feeding responses were observed in any of the test crabs while all of the controls were positive. A second series of bioassays was designed to determine the onset of inhibition. The crabs were placed in seawater and stimulated with 20 μl aliquots of a solution of 3 mM taurine and 1 μM quinone. The stimulus was administered at 2 sec intervals to alternate antennules. Inhibition of the "feeding response" was observed at approximately 10 sec. The naphthazarin derivatives were apparently more potent than the juglone derivatives. We interpret these results as indicative of a "cryptic odor" function; the crabs cannot detect the feeding stimulant after a brief exposure to the quinone.

Many higher plants contain juglone or other hydroxynaphthoquinones or benzoquinones. These compounds also occur in fungi, lichens, pholangids, millipedes, and insects. 1,4-benzoquinones are the most common ingredient of insect defensive secretions and the 2,5-substituted 1,4-benzoquinones are characteristic of fungi. A similar "cryptic odor" function may be predicted for these compounds.

Norris (1969) compared the feeding deterrent activity of a number of substituted naphthoquinones. Juglone (1) and naphthazarin (2) were the most potent inhibitors. The apparent effectiveness of the hydroxy groups in the 5- or 5,8-positions in these naphthoquinones suggests an examination of the function of the major group of secondary plant metabolites, the flavones (5) (Harborne, 1972) which have a marked structural similarity.

Whittaker and Feeny (1971) predict "that research into the relations of multicellular marine algae and their consumers will reveal chemical defenses and responses paralleling those of higher plants and animals on land." The most likely candidates to fulfill this prediction are the highly halogenated hydrocarbons that are synthesized by algae and stored in the tissues of the herbivorous gastropod, *Aplysia californica* (Faulkner and Stallard, 1973; Faulkner et al., 1973). We would add to the prediction of Whittaker and Feeny that research into the relations of many marine invertebrates and their predators may reveal allomones. Some of the "natural products" of marine invertebrates that have been recently characterized and that may have this function are the halogenated antibiotics that have been isolated from sponges (Sharma, Vig, and Burkholder, 1970; Fattorusso, Minale, and Sodano, 1972; Moody et al., 1972; Anderson and Faulkner, 1973). Steroid saponins that are toxicants or irritants have been characterized from holothuroids and starfish (Yasumoto, Nakamura, and Hashimoto, 1967; Tursch et al., 1967; Roller et al., 1969; Tursch, Cloetens, and Djerassi, 1970; Turner, Smith, and Mackie, 1971).

We recall a simple demonstration by the late C. F. A. Pantin of the sensitive chemosensory capability of sea anemones for saponin. The nematocysts of sea anemones require both a mechanical and a chemical stimulus for discharge. One can brush the surface of a sea anemone's tentacles with a clean glass rod without effecting any discharges. If, however the glass rod is first dipped into a dilute saponin solution, a massive discharge is effected.

An observation by Clark (1921) suggests the existence of allomones in crinoids. He discusses the avoidance of comatulid crinoids by fish and suggests the activity of glands at the base of the tentacles. The comatulids are unique in containing both polyhydroxyanthroquinones and aromatic polyketides (Kent, Smith, and Sutherland, 1970; Smith and Sutherland, 1971).

MARINE KAIROMONES

As in the terrestrial environment, invertebrates utilize chemical cues to locate hosts or to warn of predators. Davenport (1966) demonstrated the response of commensal polynoid polychaetes to a "host factor" in the water draining from tanks containing the host species of starfish. In an electrophysiological analysis of the antennular chemoreceptors of two commensal shrimps, Ache and Case (1969) demonstrated the specificity of the response to "host water" from the specific hosts, *Haliotis* spp. and *Strongylocentrotus* spp.

Predatory starfish induce an escape response in a variety of molluscs (Feder, 1967), and these behavioral responses probably effectively reduce the predation on these species that can detect the predator (Feder, 1963). The active materials in extracts of the starfish *Marthasteria glacialis* and *Asterias rubens* which induce the escape response have been shown to be steroid saponins (Mackie, Lasker, and Grant, 1968).

The threshold for response by the snail, *Buccinum undatum* is $0.2-0.4 \times 10^{-9}$ M (Mackie, 1970), and the structure of these steroid glycosides has been determined (Turner et al., 1971).

A behavioral bioassay of one of the orthoquinones derived from L-DOPA, dopachrome, utilizing the feeding response of the lined shore crab *Pachygrapsus crassipes* indicated that this quinone might also be a "cryptic odor." Electrophysiological studies, however, demonstrated that these results were misleading. Utilizing a preparation of the dactyl chemoreceptors of the spiny lobster *Panulirus interruptus*, we detected chemoreceptors for this quinone that were about a hundred times as sensitive as the general amino acid receptors in this preparation (Figure 2). While we have not explored the range of specificity of these receptors, the results suggest that these crustaceans, the natural prey of the octopus, have evolved a mechanism for detecting the presence of the predator. Our results with the bioassay likely reflect a priority of responses to the two chemical stimuli (Kittredge, Takahashi, and Lindsey, unpublished data).

PHEROMONES

Unicellular chemical communication, analogous to Haldane's primordial protistan communication, is evident in the conjugation of ciliates. The microconjugant of a peritrichous ciliate, which is free swimming, can identify the macroconjugant, which is sessile, by chemicals released by the latter. Although evidence for

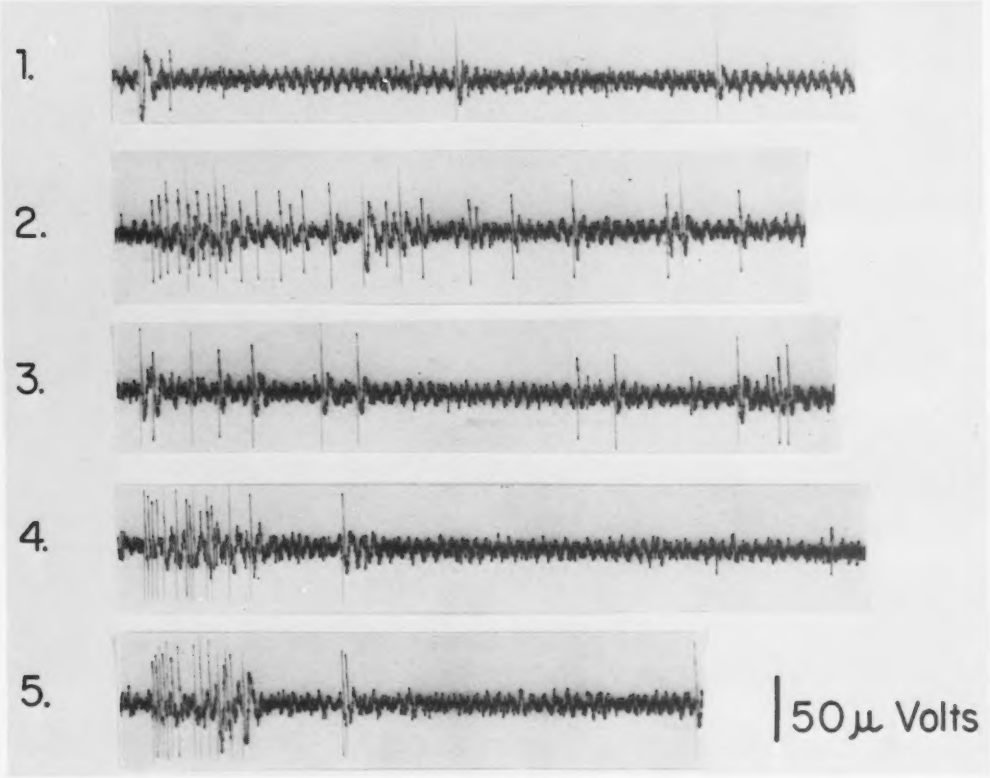

FIGURE 2.—Electrophysiological recordings from the dactyl chemoreceptors of a spiny lobster, *Panulirus interruptus*. (1) Seawater blank, (2) 10^{-5} M dopachrome in seawater, (3) Persisting spikes in dopachrome receptors (continuation of 2), (4) 10^{-3} M taurine in seawater, (5) 10^{-3} M taurine after dopachrome and a seawater wash.

the presence of a large number of agents chemotropic for male gametes exists (Machlis and Rawitscher-Kunkel, 1963), only two have been chemically characterized. Sirenin, the active compound produced by the female gametes of the water mold *Allomyces*, has been isolated and characterized as an oxygenated sesquiterpene (Machlis et al., 1966), and its structure has been uniquely established (Machlis, Nutting, and Rapoport, 1968). It is active in attracting male gametes at 10^{-10}M. The corresponding work from the marine field resulted in the characterization of the active substance released by the female gametes of the brown alga *Ectocarpus siliculosus* as allocis-1-(cycloheptadien -2′, 5′-yl)-butene-l (Müller et al., 1971). The receptor sites on the male algal gametes evidence a low level of specificity. Many lower hydrocarbons, esters, alcohols, and aldehydes, at higher concentrations, will mimic the natural compounds in attracting male gametes (Cook, Elvidge, and Bentley, 1951; Müller, 1968; Hlubucek et al., 1970).

Though many efforts to demonstrate a chemotactic response by mammalian sperm to substances from eggs have yielded negative results, such attraction does occur in marine forms. Sperm of the thecate hydroids *Campanularia flexuosa* and *C. calceolifera* respond to a substance issuing from the aperture of the female gonangium. The response is species specific (Miller, 1966). Observations by Dan (1950) suggest the activity of a similar substance from the eggs of the medusa *Spirocodan saltatrix* on the sperm of this species. The first examples of sperm chemotaxis in vertebrates are described in papers on fertilization in the herring *Clupea* by Yanagimachi (1957) and in the bitterling *Acheilognathus* by Suzuki (1961).

The attraction of the amoeboid form of the slime mold *Dictyostelium discoideum* during the aggregation phase which results in the formation of a multicellular "slug" represents the best studied protistan communication. The attractant is cyclic adenosine monophosphate (Konijn et al., 1968; Barkley, 1969). Pulses of cyclic AMP radiate out through the soil moisture at 5 min intervals from the center of a growing aggregation. The gradient and the pulse nature of the signal are maintained by each inward streaming amoeba. Each amoeba secretes a phosphodiesterase to break down the cyclic AMP and, on sensing a pulse of cyclic AMP, emits its own pulse of cyclic AMP about 15 sec after receiving a signal (Cohen and Robertson, 1971; Robertson, Drage, and Cohen, 1972). Bonner (1969) has indicated the likely course of the evolution of this communication in the social slime molds. Soil bacteria, the food of the solitary predecessors of the slime mold amoeba, secrete cyclic AMP. It is reasonable to assume that a mechanism which initially increased the feeding success of these amoebas developed, due to selective pressure, the requisite high sensitivity of response to a chemical signal necessary for aggregation. This capacity then facilitated the evolution of the social species. This is very close to Haldane's premise of the evolution of chemical communication prior to the evolution of metazoans. In further support of Haldane's premise of the lineage of hormones, after aggregation is complete the "metazoan" slug phase migrates to the soil surface and then certain cells differentiate into stalk cells which will eventually support the spore head. Cyclic AMP is apparently the chemical signal for the developmental differentiation of some cells into stalk cells (Bonner, 1970).

The recent rapid growth of our understanding of pheromone communication in insects was founded on half a century of acute biological observations which implicated the existence of chemical messengers. The isolation and chemical characterizations of a growing number of pheromones, and the concomitant behavioral studies, have provided the basis for our appreciation of the role of chemical communication in the life cycle of many species. Among the many recent reviews are those of Beroza (1970) and Jacobson (1972). Electrophysiological investigations of chemoreception in insects have demonstrated that the receptor cells may be divided into two groups, either "specialists" or "generalists" (Yamada, 1970). Among the "specialists" are the pheromone receptors and the receptors for specific secondary plant substances that act as phagostimulants (Schoonhoven, 1968). While remarkable success has been achieved in recording the response of single receptor cells as well as the summed receptor potential of all the antennal chemoreceptors (electroantennogram) these workers have had to contend with a technical problem inherent in studies with this material. Evaluation of the response of a chemosensory organ

or a single cell is difficult when the stimulant must be presented in the gas phase. Each species of stimulant molecule must partition between the gas phase and an aqueous film. The active concentration at the receptor membrane is unknown. A study of the physiology of pheromone reception by aquatic organisms would avoid this limitation.

A survey of the literature reveals that, as in the field of entomology, there exists a broad basis of behavioral observations suggesting the role of chemical communication in the aquatic environment. These studies suggest that marine invertebrates are primarily dependent on chemoreception for information from their environment. The input is composed of a broad spectrum of chemical messages ranging from species specific pheromones eliciting stereospecific responses, e.g., mating behavior, epidemic spawning, aggregation, or alarm behavior, through those kairomones triggering metamorphosis or migration to the cues indicating the proximity of predators or prey.

The closest parallel to insect pheromone communication observed in marine organisms are the sex pheromones of marine crustacea. The first experimental demonstration of "chemical recognition" by marine crustacea is the description of the behavior of male copepods *(Labidocera aestiva)* by Parker (1902). In a series of elegantly simple experiments he demonstrated that "they [the females] probably give rise to some substance that serves as a scent for the males; in other words, the males are probably positively chemotropic toward the females." Moreover Parker noted that "they [the males] seldom pass near the tube without some characteristic reaction. Usually they made one or two quick circles as they swam by, or even a somersault-like motion; these were observed fifteen times when the females were in the tube, never when they were not." Lillelund and Lasker (1971) observed similar swimming behavior in male *Labidocera jollae*. Although *L. jollae* females swim in a seemingly random pattern with only occasionally looped excursions, the males frequently vary their random course of a few seconds duration by swimming in circles, covering a small area intensively. Of greater interest was the observation that rather than circles, the path of the males often resembled a curtate cycloid. The males occasionally progressed for several centimeters in this curtate cycloid path (Figure 3). These observations, although obtained during feeding studies, suggest an important aspect of the physiology of pheromone response in small crustacea—the mechanism of sensing a chemical gradient. Crisp and Meadows (1962) have stated that, because of the small distance between the chemosensory organs of barnacle cyprid larvae, these larvae cannot detect a chemical gradient and thus

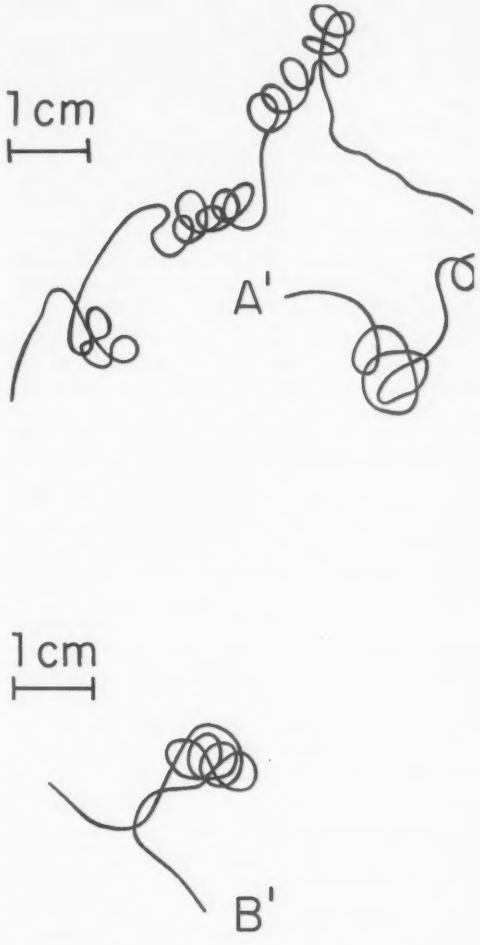

FIGURE 3.—Swimming behavior of a male copepod *Labidocera jollae*. A′ and B′ mark the termini of the tracings. The upper trace shows both an occasional circular swimming course, progression in a curtate cycloid course and "doubling back." The lower trace is an extreme example of the "doubling back" behavior.

cannot exhibit chemotactic behavior. This reasoning has been applied to all small marine crustacea including copepods. From the above observations it is apparent that the reasoning of Crisp and Meadows is invalid for *Labidocera* and probably for other small crustacea. The critical dimension is the diameter of the circular course, not the dimensions of the organism. A circular swimming pattern in a concentration gradient of a stimulant would result in a sinusoidal variation in the signal intensity. Alteration of the radius of curvature of the swimming course in response to this sinusoidal input would result in cycloidal progression in the gradient. It appears from the observations of the behavior of male *L. jollae* in the feeding experiment that a threshold level of stimulant will trigger a circular swimming pattern, if this circular course results in the detection of a gradient, the circular course will become a curtate cycloid with the ratio of the major to the minor radius being a function of the intensity of the gradient. A frequent observation is a doubling back. If several progressions of the cycloid result in loss of the gradient signal (as must frequently occur in a medium in which the dimensions of the turbulent flow are of the same scale as the swimming pattern), the swimming plots indicate that the male *Labidocera* can effectively loop back through the area where the signal was initially detected (Figure 3). These observations indicate some power of spatial orientation and short term memory in *Labidocera*.

In crabs the male is attracted to the premolt female. During this attraction phase he may display a stance characterized by standing on the tips of his dactyls and elevating his body. He will seize the premolt female and place her below his body. He will protect her during the vulnerable molting period and they copulate immediately after molting. Ryan (1966) demonstrated pheromone communication in this interaction. Water from a tank containing a premolt female *Portunus sanguinolentus*, when added to a tank containing a male of this species, elicited the premolt stance. Evidence that the pheromone is released from the antennule glands was provided by sealing these glands and noting the absence of the stimulating factor.

We have examined this pheromone communication in the lined shore crab, *Pachygrapsus crassipes*. We isolated an active substance and found that it behaved chromatographically like the molting hormone, crustecdysone. Pure crustecdysone is active in stimulating all of the precopulatory behavior of male lined shore crabs from an early search behavior through the display stance to seizing the female. The threshold for stimulating the stance is 10^{-13} M (Kittredge, Terry, and Takahashi, 1971). Confirmation of the identification has been obtained by injecting tritiated crustecdysone into intermolt female Dungeness crabs *(Cancer magister)* and detecting its release as the females entered premolt. Recently we have detected the presence of two additional pheromones released by the female lined shore crabs. Compound A is released in addition to crustecdysone prior to molt. After molting compound A is no longer released into the water, but, if the female is held in isolation from male crabs, a second compound, B, is released. It is likely that the postmolt female has a different message to transmit.

Evolutionary biologists concerned with the inception of pheromone communication have long been puzzled by a dilemma. This chemical communication implies two new capabilities, that to synthesize a messenger compound and the ability to receive the message and translate it into a behavioral response. The improbability of the simultaneous occurrence of these two *de novo* events suggests a stepwise sequence. The observation that the molting hormone of crustacea can function as a sex pheromone indicates that the primordial Arthropoda, through an evolutionary sequence that resulted in structuring the receptor site for the hormones on chemosensory membranes, were able to initiate pheromonal communication (Kittredge and Takahashi, 1972).

SUMMARY

Evidence from the literature supports Haldane's premise that chemical communication is the most primitive form of communication and thus the lineal predecessor of synaptic transmission and hormone function. Transducers of environmental chemical information have likely evolved in response to the metabolic products released by their prey and by competitive organisms. This coevolution of "natural products" and the respective transducers has existed from the earliest metabolic product that happened to be a membrane irritant to the

present. We thus consider it likely that most of the "natural products," not only of terrestrial plants, but also of marine plants and invertebrates, function as allomones, kairomones, or pheromones. Faulkner and Anderson (In press) have provided a review of the chemistry of the "natural products" of marine organisms.

Conceptually, in such a "chemical environment" the most effective protection from a predator would be a "cryptic odor," an irritant that disrupts chemoreception. These cryptic odors may be released into the environment, as is the active component of octopus ink, they may exist in the epidermal tissues or glands where they would function at the inception of attack, or they may be contained in the eggs or larvae. Most sessile marine invertebrates reproduce by epidemic spawning, the simultaneous release of the gonadal products of an entire local population of a species. Most sessile marine invertebrates are also filter feeders. The prime advantage of epidemic spawning is the enhancement of fertilization. However, in the densely populated benthic environment, a heavy loss of eggs or larvae to filter feeders may occur. The presence of a "feeding inhibitor" in the eggs or larvae would reduce such losses. Reiswig (1970) reported that they observed epidemic spawning of the sponge *Neofibularia nolitangere* on a Jamaican reef. At the time they were measuring the water pumping rate of other sponges. When the epidemic spawning of *N. nolitangere* started, the pumping rate of the species under study, *Verongia* sp, abruptly decreased and remained negligible for 2 days. *N. nolitangere* is known to contain toxic substances.

The evidence for chemical cooperation, from gamones to sex pheromones, suggests a pattern of increasing complexity in the function of chemical cues. The behavioral response of even a "simple" crustacean to a chemical gradient appears to involve at least some short term "memory" or a type of "chemical-spatial" sense that we have not observed in such clear-cut form in any other organism.

The study of the chemical ecology of the marine environment is scarcely in its infancy. The chemical characterization of some of the intraspecific and interspecific messages in the sea and the physiology of their perception are challenges. Solutions to these paired problems will provide insights into the evolution of chemical transduction and perhaps expose a hierarchy of perception from membrane irritation to synaptic transmission.

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A SIMPLE BIOECONOMIC FISHERY MANAGEMENT MODEL: A CASE STUDY OF THE AMERICAN LOBSTER FISHERY[1]

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ABSTRACT

The pressures of world economic expansion have led to more intensive exploitation of living marine resources as a source of protein. The exploitation of these common property resources leads, in many cases, to overfishing and depletion. This paper attempts to develop a simplified management tool to prevent overexploitation and depletion of a fishery resource. A general resource model is postulated embracing both biological and economic relationships. This bioeconomic model approximates the operation of a fishery under free access to the resource. A Schaefer type yield function is combined with a linear demand function, and other standard economic relationships and simulations are performed to evaluate the model. Using computer simulation, we imposed five management strategies on the case example, the American lobster fishery. These strategies include (1) freezing fishing effort by raising license fees; (2) reducing fishing effort to that necessary to harvest at the maximum sustainable yield by raising license fees; (3) reducing fishing effort to an "economic optimum" where marginal cost of doing business is equal to marginal revenue from sales by raising license fees; (4) instituting a "stock certificate plan" where individual fishermen would own portions of the resource and trade catch certificates on the open market; however, the total number of catch certificates would not exceed the maximum sustainable yield; and (5) doing nothing. The economic impact in terms of catch, fishing effort, number of fishermen, ex-vessel prices, license revenues, and returns per boat and fishermen were computed for each management strategy so that policymakers and industry leaders could see the alternative consequences of these management positions. The simplified model also is available for use in evaluation of other management schemes that might be suggested.

In the past few years the world community has become increasingly aware of the sea and its resources. The pressures of world economic expansion have led to more intensive exploitation and, at the same time, to increasing concern over the marine environment. Many management strategies used to protect these resources from overexploitation have resulted in inefficient use of gear and equipment as shown by Crutchfield and Pontecorvo (1969). The purpose of this paper is to develop a bioeconomic model of living marine resource exploitation which can be used to assess the economic impact of alternative management strategies for the U.S. inshore American lobster fishery. The U.S. American lobster fishery is a classic case of rapid increases in consumer demand impinging upon a limited resource (Bell, 1972). It should be made quite clear that this analysis is intended to predict the effects of alternative actions without recommending any specific policy.

SPECIFICATION OF THE GENERAL RESOURCE USE MODEL

Before we are able to evaluate the economic impact of various management strategies, it is necessary to develop a general bioeconomic model of how a fishery functions. The following general model has been developed by Fullenbaum, Carlson, and Bell (1971):

$$X = f(X, Kx) \tag{1}$$

$$Kx = Kg(X, K) \tag{2}$$

or

$$x = g(X, K)$$

$$C = K\tilde{\pi} \tag{3}$$

[1] This article was first submitted for publication 7 August 1972. At that time, all data were as current as could be obtained for purposes of the analysis. The views of the authors do not necessarily represent the official position of the U.S. Department of Commerce.

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$$\pi = pKx - C = pKg(X,K) - K\tilde{\pi} \quad (4)$$

$$\dot{K} = \delta_1\pi, \pi>0 \quad (5)$$

$$\delta_2\pi, \pi<0$$

In the above system, X is the biomass; K equals the number of homogeneous operating units or vessels; x is the catch rate per vessel; C is total industry cost (in constant dollars) or total annual cost per vessel multiplied by the number of vessels; $\tilde{\pi}$ is equal to total annual cost per vessel (in constant dollars) or opportunity cost;[4] π is industry profit in excess of opportunity cost; p is the real ex-vessel price; and δ_1, δ_2 represent the rates of entry and exit of vessels, respectively. Equation (1) represents the biological growth function in which the natural yield or net change in the biomass ($\dot{X}$) is dependent upon the size of the biomass, X, and the harvest rate, Kx. X reflects the influence of environmental factors such as available space or food, which constrain the growth in the biomass as the latter increases. The harvest rate or annual catch, Kx, summarizes all growth factors induced by fishing activity. Equations (2) present the industry and firm production function for which it is normally assumed that $\frac{\partial g}{\partial X} \equiv g_1 > 0$ and $\frac{\partial g}{\partial K} \equiv g_2 < 0$.[5] In other words, catch per vessel increases when the biomass increases and declines when the number of vessels increases. Equations (3) and (4) are the industry total cost and total profit function, respectively. Equation (5) is a very important equation since it indicates that vessels will enter the industry when excess industrial profits are greater than zero (i.e., greater than that rate of return necessary to hold vessels in the fishery, or the opportunity cost) and will leave the fishery when excess industrial profits are less than zero (i.e., below opportunity cost).

The equilibrium condition for the industry ($\pi = 0$) may be formulated as shown below:

$$p = \frac{\tilde{\pi}}{g(X,K)} \quad (6)$$

Equation (6) merely stipulates that ex-vessel price is equal to average cost per pound of fish landed (i.e., no excess profits).

There are two important properties of the system outlined in (1) - (5). First, the optimum size of the firm is given and may be indexed by $\tilde{\pi}$. Thus, the firm is predefined as a bundle of inputs.[6] Second, the long-run catch rate per vessel per unit of time is beyond the individual firm's control.[7] It is, in effect, determined by stock or technological externalities.[8] Finally, we are assuming that the number of homogeneous vessels is a good proxy for fishing effort. Alternatively, we may employ fishing effort directly in our system by determining the number of units of fishing effort applied to the resource per vessel. This will be discussed below.

A QUADRATIC EXAMPLE OF THE RESOURCE USE MODEL

By combining the more traditional theories depicting the dynamics of a living marine resource with some commonly used economic relations, we may derive a quadratic example of the general model specified above. This example effectively abstracts from complications such as ecological interdependence and age-distribution-dependent growth of the biomass on the biological side and, furthermore, assumes the absence of crowding externalities (i.e., $g_2 \equiv 0$) in the production function on the economic side.

[4] Opportunity cost is defined as the necessary payment to fishermen and owners of capital to keep them employed in the industry or fishery compared to alternative employment or uses of capital.

[5] In some developing fisheries, it is possible that $g_2 > 0$. For example, in the Japanese Pacific tuna fishery, intercommunication between vessels may increase the catch rate as more vessels enter the fishing grounds.

[6] In other words, because we are dealing with a long-run theory of the industry, we are assuming that variations in output result from the entry or exit of optimum-sized homogeneous vessels.

[7] We have implicitly assumed that such short-run changes as longer fishing seasons, etc., are all subsumed in a long-run context. Normally longer fishing seasons, for example, do not change catch rates per unit of time fished; nor do they change costs per unit of time fished. They do, however, change the effective level of K.

[8] A technological externality exists when the input into the productive process of one firm affects the output of another firm. In the context of fishing, an additional firm or vessel entering the fishery will utilize the biomass (as an input) and, as a result, in the long run will reduce the level of output for other vessels in the fleet. (See Worcester (1969)).

The dynamics of a fish stock may be depicted by the logistic growth function (Lotka, 1956).[9]

$$X(t) = \frac{L}{1 + Ce^{-KLt}} \text{ where } L>0, C>0, k>0, \quad (7)$$

where L, C, and K are assumed to be environmental constants. Differentiating (7) and substituting we obtain,

$$\dot{X} \equiv \frac{dX}{dt} = kLX - kX^2 \equiv aX - bX^2 \quad (8)$$

where $a = kL$, $b = k$.

If (8) is set equal to zero, we may solve for the nonzero steady-state biomass, a/b (i.e., L). Alternatively, the limit of $X(t)$ as $t \to \infty$ yields identical results. The maximum of (8) occurs when X is equal to $a/2b$. Thus

$$\max \frac{dX}{dt} = a^2/4b \quad (9)$$

The introduction of fishing (i.e., harvest or Kx) is assumed to have no interactive effects, so that the instataneous growth rate is reduced by the amount harvested:[10]

$$\frac{dX}{dt} = aX - bX^2 - Kx. \quad (10)$$

The economic component of the model requires the exact specification of an industry production function and an industry revenue relationship. One hypothesis regarding the fish catch is that the proportion of the biomass caught is a direct function of the number of vessels (or equivalent fishing effort) exploiting a given ground.[11] Thus, the total harvest rate is given as,

$$Kx = rKX \quad (11)$$

where r is a technological parameter.[12] Finally, the total revenue function for the industry may take the following form:

$$pKx = (\alpha - \beta Kx)Kx. \quad (12)$$

Equation (12) merely stipulates that the total revenue is a quadratic function of total landings, Kx. Dividing through by Kx will give us the familiar demand function where ex-vessel price is inversely related to landings, holding all other factors constant.[13] With total costs equal to $K\pi$, the profit function becomes

$$\pi = (\alpha - \beta Kx)Kx - K\tilde{\pi}. \quad (13)$$

Given these formulations, the system in (10) - (13) can be reduced to two steady-state functions. The first, which condenses all relevant biotechnological factors, is the ecological equilibrium equation. It plots the relationship between the biomass and the number of vessels (or fishing effort) needed to harvest the yield such that the biomass is in equilibrium. We can derive this equation by setting $\dot{X}$ equal to zero, substituting (11) into (10), and solving for K in terms of X:

$$K = \frac{1}{r}(a - bX). \quad (14)$$

Similarly, the second equilibrium function plots the relationship between X and K under a zero profit state, i.e., under conditions that $K = 0$, or that there is no entry to or exit from the fishery. Thus, by setting (13) equal to zero and substituting (11) into (13), we obtain

$$K = \frac{\alpha}{\beta r X} - \frac{\tilde{\pi}}{\beta r^2 X^2}. \quad (15)$$

---

[9] Graham (1935) was the first biologist to apply the logistic growth model to exploited fish populations.

[10] Schaefer, (1954) was the first population dynamicist to develop the function specified in equation (10).

[11] Alternatively, one could assume that the proportion of the biomass caught declines as the number of vessels increases:

$$Kx = [1 - (1 - t)^K]X. \qquad 0<t<1$$

With this specification, t represents the proportion of the biomass taken by the first vessel and also represents the percentage taken by each succeeding vessel of the remaining biomass. This form was first developed by E. W. Carlson (1970. An economic theory of common property resources. Unpubl. manuscr. Econ. Res. Lab., Natl. Mar. Fish. Serv., NOAA College Park, Md.).

[12] A reviewer of this article has pointed out that r is not likely to be constant over any large number of years. Since there are no time series observations on X, r cannot be tested to see whether it varies over time or is a constant. In this case, we are merely following the simplified Schaefer model.

[13] Such complicating factors as per capita income and its influence on ex-vessel prices can be introduced later as changes in the parameter, α.

These two curves are plotted in Figure 1.[14] Their intersection at (X^*, K^*) denotes bioeconomic equilibrium. The direction of the arrows describes the qualitative dynamic changes of a point in phase space. Figure 1 represents the general case of exploitation. When (15) is combined with (14), however, we can simulate either nonexploitation (Figure 2) or extinction as a possible dynamic result (Figure 3).[15] The state of the fishery—exploited, unexploited, or extinct—depends upon the parameters a, b, r, β, $\tilde{\pi}$, and α and their interrelationships. This completes our general model of how a fishery functions. Now let us turn to a specific application of the model.

AN EMPIRICAL CASE STUDY: THE U.S. INSHORE AMERICAN LOBSTER FISHERY

The U.S. inshore American lobster fishery—principally located off the coast of Maine—represents a good case study for a number of reasons. First, the American lobster is considered a high quality seafood item and is a popularly consumed species for which demand has been increasing rapidly (Bell, 1972). Second, because of intensive fishing pressure, the resource has shown signs of overexploitation.[16] Third, the inshore lobster fishery is one of the few grounds for which enough data are available so that some rough measures of needed biological and economic parameters can be derived. Fourth, according to Dow (1961),[17] the inshore lobster fishery is a relatively closed population as our production model assumes. Last, we believe that over the long run the American lobster population has not had a great divergence from the steady-state model employed in our analysis. The gross divergence from the steady-state assumption is significant only when fishing effort changes dramatically from period to period. For modest changes in fishing effort, the steady-state assumption will not yield biased estimates. A check on the fishing effort series for the American inshore northern lobster fishery reveals a steady and gradual increase. The alternative methods of Pella and Tomlinson (1969) do yield biased parameters due to nonlinear fitting methods. Gulland's (1961) method yields biased parameters since effort is averaged and then used as an independent variable. Therefore effort in period t is not independent of effort in period $t + 1$ which violates classical statistical assumptions underlying least squares. Also the predictive value (using the steady- state assumption) or goodness of fit is certainly at an acceptable level, $R^2 = 0.962$ (infra). Our discussion will be subdivided on the basis of production-related and demand-related estimates.

The Production Function and the Supply of American Lobsters

There are four parameters on the supply side for which initial estimates are required: a, b, r,

[14] In steady state, the reader should be aware that we have not constrained the population stock to its initial size or any other size. Using the Schaefer model (i.e., steady state), the stock size varies inversely with fishing effort, T. Even in a dynamic context, the biomass would asymptotically approach the steady-state solution.

[15] It should be pointed out that Schaefer (1954) discusses economic transitional states which are very similar to the bioeconomic model presented in this paper. He states:

> "To arrive at a particular function to describe the change of the intensity of fishing with the size of the population, we may consider that the incentive for new investment is proportional to the return to be expected, in which case there will be a linear relation between the percentage rate of change of fishing intensity and the difference between the level of fish population and its economically critical level, b. This function will, then, be
>
> $$\frac{dF}{dt} = k_3 F(P - b) \quad \text{------ (11)}$$
>
> where k_3 is a constant."

His process of transitional states is implicit in our diagrams in Figure 3 since adjustment (i.e., transitional states) will occur anywhere in phase space to the equilibrium values where $\dot{X} = 0$ and $\dot{K} = 0$.

[16] U.S. landings of trap-caught American lobsters increased from approximately 23 million pounds in 1950 to a peak of over 29 million pounds by 1957. Since 1957 landings have fallen off, reaching a low of 22 million pounds in 1967. In 1969 lobster production had recovered to 26.9 million pounds. Despite the poor performance of production over the 1950-69 period, the number of lobster traps fished per year (i.e., a proxy for fishing effort) has increased secularly from approximately 579,000 in 1950 to over 1,060,000 in 1969. Because of these past events, several bills have been presented in the Maine Legislature to apply some sort of stringent licensing scheme to limit entry.

[17] Dow, R. 1971. Effort, environment, supply, and yield in the Maine lobster fishery. Unpublished manuscript submitted to the U.S. Fish and Wildlife Service, Washington, D.C. 125 p. (May be obtained from Sea and Shore Fisheries, Maine.)

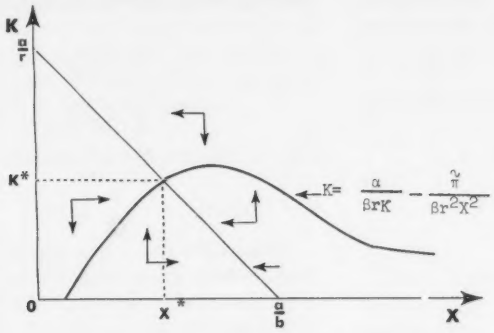

FIGURE 1.—Exploitation.

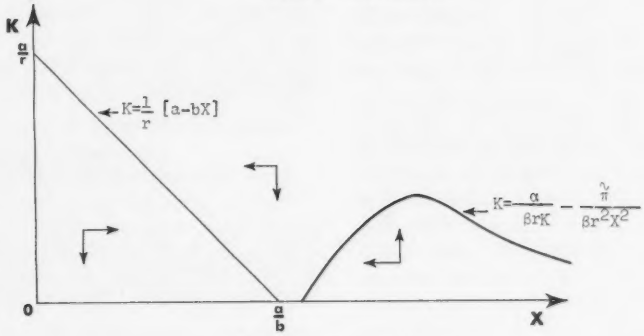

FIGURE 2.—Non-exploitation.

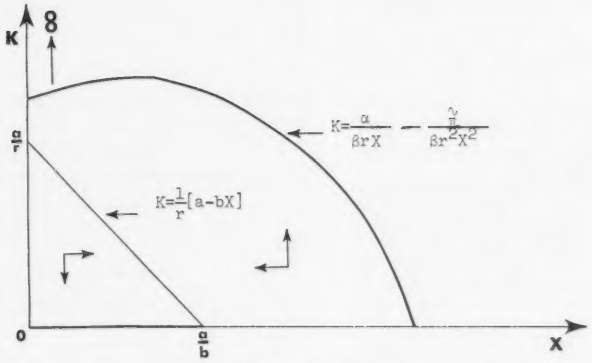

FIGURE 3.—Extinction.

and $\tilde{\pi}$.[18] The first three can be developed by combining statistical estimation and independently derived data. Assume that the biomass is instantaneously in equilibrium (i.e., $\frac{dX}{dt} = 0$). Then, taking the inverse of (14) and substituting it for X in (11), we obtain:

$$Kx = cK - dK^2 \tag{16}$$

where $$c = \frac{ar}{b},\ d = \frac{r^2}{b}$$

and $$x = c - dK. \tag{17}$$

Equation (16) is the familiar parabolic yield function postulated by Schaefer (1954).[19] Notice that both the harvest rate, Kx, and output per vessel, x, may be specified solely in terms of the number of vessels or fishing effort. Similarly, the common property resource externality, as given in (17), is a function only of the level of K. Over a longer period of time the basic assumption underlying equations (16) and (17) may reflect a valid representation; i.e., effort or K is the only instrumental variable affecting output. There are three different parameters embedded in estimates of c and d. The only way that a, b, and r can be derived is if some independent biological information is given. More specifically, suppose that we have an estimate of the biomass consistent with maximum sustainable yield, call it $\hat{X}^\circ$. Since $\hat{X}^\circ$ is equal to $a/2b$, it follows that the following parameters may be estimated (designated by $\hat{}$):

$$\hat{r} = \hat{c}/2\hat{X}^\circ \tag{18}$$

$$\hat{b} = [\hat{d}/\hat{r}^2] - 1 \tag{19}$$

$$\hat{a} = \hat{c}\hat{b}/\hat{r}. \tag{20}$$

Thus, (17) will be estimated subject to one modification concerning the introduction of an environmental variable. Several biologists, including Dow et al. (1961),[20] have argued that a long-term trend of declining seawater temperature is partially responsible for the decline in U.S. coastal catches.[21] It will be assumed in this study that seawater temperature (°F) affects the a term in the growth function so that,

$$\frac{dX}{dt} = a(^\circ\mathrm{F})X - bX^2, \tag{21}$$

where °F is equal to the mean annual seawater temperature, in degrees Fahrenheit Boothbay Harbor, Maine, with $\frac{\partial a}{\partial(^\circ\mathrm{F})} \equiv a' > 0$. Seawater temperature can easily be incorporated into (17) in the following way:

$$x = c' - dK + z(^\circ\mathrm{F}), \tag{22}$$

where z represents the change in output per boat as a result of a one-degree change in water temperature.[22]

Data on the number of traps fished per year for the entire inshore American lobster fishery

[18] An alternative approach suggested by Thomas (1970) uses the Beverton-Holt model in developing a yield/recruit relationship. However, because a stock-recruitment equation is not specified, it cannot be incorporated into our bioeconomic model at this time.

[19] The reader should recognize that it does not follow that (17) can be derived from a generalized growth equation [$\dot{X} = F(X) - Kx = 0$] and production function $Kx = f(X,K)$. Only under certain specifications of the previous two functions will it follow that x can be defined as a unique function of K (or X) only. In addition, this production function could have been more generally specified as $Kx = rK^\alpha X^\beta$. However, two compelling factors make it desirable to employ this function. First, there are no observations on the biomass, X, so that empirical tests cannot be made to estimate ß. Second, the equation $Kx = rKX$ combined with the logistic gives an excellent empirical fit to past behavior in the fishery (i.e., $R^2 = 0.962$ for yield function equation 23). In addition, Schaefer makes the same assumption as we did, and this assumption is generally accepted as plausible for most fisheries. In conclusion it is difficult for us to imagine how a different assumption could lead to superior predictive results (i.e., goodness of fit).

[20] Dow, R., D. Harriman, G. Pontecorvo, and J. Storer. 1961. The Maine lobster fishery. Unpublished manuscript submitted to the U.S. Fish and Wildlife Service, Washington, D.C. 71 p. (May be obtained from Sea and Shore Fisheries, Maine.)

[21] Higher seawater temperature can affect the natural yield of lobsters by providing a climate in which molting is facilitated. A larger number of molts will tend, *ceteris paribus*, to increase the yield associated with any given level of the biomass.

[22] Implicit in the way the effect of seawater temperature is measured is the relationship:

$$[a = a_0 + d(^\circ\mathrm{F})].$$

are available for the 1950-69 period (see Appendix Table).[23] Output per trap was regressed against the number of traps and seawater temperature on the assumption that the number of traps per boat was constant. The regression estimates yielded the following results:

$$x = -31.82 - 0.00002807(T) + 1.846(^{\circ}\text{F}) \quad (23)$$

$$(6.55) \qquad (4.99)$$

$$R^2 = 0.962$$

$$\text{D-W} = 2.38$$

where $T = 562.8(K)$: $\hat{a} = 0.0156$; $\hat{c} = -31.82 + 1.846(^{\circ}\text{F})$. In (23), T is equal to the number of traps fished per year, and t-ratios are in parentheses.[24] Both T and °F are statistically significant at the 5% level and exhibit the correct sign; the Durbin-Watson statistic indicates no significant autocorrelation.

The only step required to obtain the biotechnological parameters is an estimate of the biomass consistent with maximum sustainable yield. It has been calculated that (assuming a temperature of 46°F) the fishable stock of U.S. inshore American lobsters consistent with maximum sustainable yield is equal to 31 million pounds.[25] For the Gulf of Maine (where most of the resource is located), estimates of the biomass were made through sampling experiments.[26]

Finally, on the basis of recent cost studies, we have derived an estimate of $\hat{\pi}$ for 1966 equal to $12,070.[27, 28] Therefore, on the supply side, the estimated parameters for 1969 are the following:

$$\hat{a} = 1.85379$$
$$\hat{b} = 2.9899 \times 10^{-8}$$
$$\hat{r} = 5.1562 \times 10^{-4}$$
$$\hat{\pi} = \$13{,}191 \text{ (see footnote 27).}$$

The Demand Function for American Lobsters

Only knowledge of $\hat{a}$ and $\hat{\beta}$ is needed in order to complete the empirical component of the study. The estimation procedure is rather straightforward. We may specify the following demand function for all lobsters:

$$\frac{C}{N} = F - m(P'/\text{CPI}) + g(Y/N) \quad (24)$$

where C is equal to consumption of all lobsters, P' is the money ex-vessel price of American lobsters, Y is aggregate U.S. personal income (1967 prices), N is U.S. population, and CPI is the consumer price index. Since there are no exports of lobster, the following identity holds:

$$C = I + Q_o + Q_{\text{in}} \quad (25)$$

where I, Q_o, and Q_{in} are the level of imported lobsters, U.S. production of all other lobsters, and U.S. production of inshore American lobsters, respectively. Given (25), equation (24) may be solved in terms of P, or,

$$P = \frac{P'}{\text{CPI}} = \left[\frac{F}{e} - \frac{1}{mN}(Q_{\text{in}} + Q_o + I) + \frac{gY}{mN}\right] \quad (26)$$

If Q_o, I, Y, CPI, and N are held constant, equation (26) gives a unique relationship between the ex-vessel price of American lobsters and quantity landed.

Using data over the 1950-69 period (see Appendix Table), the parameters of equation (24) were estimated using least squares:

[23] The assumption of a constant number of traps per boat is necessary in order to solve for a coefficient on "K", and thereby, to obtain the biotechnological parameters embedded in the yield-effort relationship. The relationship for 1966, derived on the basis of cost data obtained from the National Marine Fisheries Service's Division of Financial Assistance was 562.8 traps per full-time equivalent northern lobster boat. However, it should be pointed out that when the stock is large and the catch high, it may pay to increase the number of traps per boat; therefore, this might bias the number of "standardized boats", but not total amount of effort.

[24] However, the reader should note that the empirical estimates themselves (1950-69) make no assumption with respect to the relation between K and T. x was regressed on T and °F. Only in the simulation was a relationship assumed ($T = 562.8K$).

[25] U.S. Department of the Interior. 1970. Joint master plan for the northern lobster fishery. Unpublished manuscript. 130 p. (May be obtained from the National Marine Fisheries Service, Washington, D.C.)

[26] No attempts were made to run the simulation model with varying sizes of the MSY biomass as this would unnecessarily complicate this paper which is intended to be simplistic as possible.

[27] Cost data from the National Marine Fisheries Service's Division of Financial Assistance (1966) reveal the following cost breakdown for a representative lobster boat: operating expenses, $4,965.16; fixed expenses, $1,180.20; returns to capital and labor, $5,825.48. This gives a total of $12,070.84. The latter figure was updated to 1969 by income increases in Maine to obtain $13,191.

[28] We will assume that $\bar{\pi}$ remains constant in real terms. This is equivalent to keeping our estimate of $\bar{\pi}$, $\bar{\pi}$ constant, while deflating all nominal variables on the demand side.

$$\frac{C}{N} = -0.0632 - 0.005029\left(\frac{P'}{\text{CPI}}\right) + 0.00051\,\frac{Y}{N} \quad (27)$$

(2.06) (5.38)

$R^2 = 0.816$

D-W = 0.619

All of the independent variables are significant at the 0.05 level. However, the Durbin-Watson statistic indicates the strong possibility of positive autocorrelation. Nonetheless, we will use these estimates as rough approximations to obtain the price-dependent relationship as shown in (26). Given 1969 values of exogenous variables (N = 199,100,000; Y = $567,635 million; CPI = 109.8 with a base of 1967 = 100; $Q_o + I$ = 158.8 million pounds), we have,

$$P = 1.179 - (0.99853 \times 10^{-8})Q_{in}. \quad (28)$$

Thus initial values for $\hat{\alpha}$ (1.179) and $\hat{\beta}$ (0.99853 $\times 10^{-8}$) have been obtained.[29]

[29] For purposes of simplification, the parameters of the model are all assumed constant. Certainly, one could argue that the parameters, so tacitly assumed to be constants, are at best random variables. Therefore, a stochastic treatment might be used with criteria like maximal expected present value or minimal maximum expected loss for evaluating the management alternatives rather than simple deterministic computations. Possibly, the parameters are random variables and conditional on some of the suggested management alternatives. For example, freezing effort might accelerate r, leading to shifts in season or age structure harvested, hence a change in a/b.

HOW THE MODEL WORKS: THE IMPACT OF CRITICAL VARIABLES

To illustrate the power of the model in explaining the impact of changes in critical variables, we may derive initial quantitative estimates of the ecological equilibrium and economic steady-state functions. In this section we will illustrate the power of the model in explaining the impact of changes in critical variables. The year 1969 is selected for initial quantitative estimates of the ecological equilibrium and economic steady-state functions. Table 1 shows what happens to the value of (X^*, K^*) as well as the equilibrium harvest level, $(Kx)^*$, when the following changes take place:

a) A 25% increase in opportunity costs of labor caused by the development of greater regional industrial activity;
b) A 25% increase in the supply of other lobsters traceable to the discovery of a new lobster ground;
c) A 5% increase in personal per capita income; and
d) A decrease in water temperature from 48° to 47° F.

Notice that these changes are for illustrative purposes; however they do come about on a routine basis in the real world. Perhaps 25% changes in selected variables do not come about in one year so the reader can view the new equilibrium

TABLE 1.—The impact of exogenous shocks to the inshore American lobster fishery on the effort, catch, and biomass.

	Vessels, full-time equivalent K^*	Traps E^*	Catch Kx^*	Biomass X^*
	Number	*Number*	*Million pounds*	
Initial equilibrium (1969) (computed by model)	1,936	1,089,000	28.56	28.62
New equilibrium:				
(a) Increase (25%) in opportunity cost of labor	1,531	861,718	28.1	35.6
(b) Increase (25%) in exogenous supply of lobsters	947	533,000	22.3	45.7
(c) Increase (5%) in personal per capita income	2,182	1,228,310	27.4	28.0
(d) Decline in water temperature by 1°	1,851	1,041,710	26.8	29.0
(e) Changes (a)-(d) simultaneously	905	509,356	20.7	45.9

positions shown in Table 1 to result over a period of years from the 1969 initial equilibrium. We may incorporate all of the four changes given separately in (a) - (d) to ascertain their net impact. The strength of the simulation model is that we can study the separate and combined influences on the fishery of important variables. Because we have both positive and negative influences on fishing effort, it is likely to be such that complete extinction of a particular species would be somewhat difficult.[30]

ECONOMIC IMPACT OF SELECTED MANAGEMENT ALTERNATIVES

Up to this point, we have been concerned largely with building a bioeconomic model that considers all important variables. The model is based upon the fact that open access to the American lobster fishery is permitted. However, all States restrict gear to pots and traps. Each State (Maine, Massachusetts, New Hampshire, and Rhode Island) has a minimum length requirement; permitted minimum lengths vary from 3⅛ to 3 3/16 inches. We are taking the array of existing regulations as given. We shall consider the economic impact of five alternative policies that could be adopted to manage or to limit entry to the entire American lobster fishery. These management strategies assume that some central authority such as a regional commission could impose these regulations.[31] The specific objectives of these management strategies will be discussed below. All strategies have two objectives in common which are (1) to protect the resource from overexploitation and (2) to allow maximum freedom for operators to function in a free enterprise fashion. Further, the following strategies are meant to be illustrative and do not exhaust all possible alternatives. Also, two other management strategies suggested by Reeves (1969) and Sinclair (1960) will be reviewed. As other management strategies are suggested both inside and outside government, the model formulated above may be used to predict their impact.

Some Possible Alternative Management Strategies for Inshore American Lobsters

1. *Freeze on existing (1969) fishing effort by placing a license fee on traps:* Under this scheme, the regulatory authority would calculate a license fee on traps which would keep the level of fishing effort constant despite an increase in the demand for lobsters.[32] A license fee could not be levied on the individual vessel because this would not control the number of traps fished per vessel. The increased cost of operations due to the license fee would make it uneconomical for vessels to enter the fishery even though ex-vessel prices have increased. In essence, the license fee would siphon off increased revenue (or profits) from an increase in ex-vessel prices assuming the latter increases faster than cost of operations. For purposes of illustration, let us assume that we desire to manage the inshore American lobster fishery commencing in 1974. Given the estimated trend in important variables in the fishery (i.e., $\hat{\hat{\pi}}$, I, Q_0, Y, N, CPI) to the year 1974, it would be necessary to place an estimated annual license

[30] This is subject to two qualifications. First, since we are plotting only equilibrium relationships, extinction is a possible dynamic outcome (as was mentioned previously). Second, we have implicitly assumed that in the case of American lobster, the rate of technological advance is minimal. This is a fairly realistic assumption for the inshore trap fishery. However, in general, $r = r(t)$, with $r' > 0$.

[31] With the steady-state assumption, the management policies would in fact maximize the present value of the stream of net benefits over time.

[32] The model can derive the "correct tax" (or license fee) in a number of ways. Suppose, the regulatory authority wishes to freeze effort at some specified level K^0. We can derive the equilibrium yield consistent with K^0, call it $(Kx)^0$, from the yield-effort relationship. The total tax and the tax per vessel are then respectively given by:

$$T_x = (\hat{\alpha} - \hat{\beta}(Kx)^0)(Kx)^0 - K^0\hat{\hat{\pi}}$$

$$T_x/K = \frac{[(\hat{\alpha} - \hat{\beta}(Kx))\,x - \hat{\hat{\pi}}]}{K}$$

In similar fashion, if the regulatory authority wishes to freeze effort at a level consistent with maximum sustainable yield, we can obtain the tax that will insure this level of exploitation.

The only other taxing scheme that requires further explanation is a tax that will insure marginal cost pricing. Long-run industry marginal cost can be defined as:

$\hat{\pi}/\frac{\partial Kx}{\partial K}$, where $\frac{\partial Kx}{\partial K}$ is the first derivative of (16). Total industry cost can then be redefined as,

$$\left(\frac{\hat{\hat{\pi}}}{\partial Kx/\partial K}\right)Kx$$

This expression can be substituted into the total revenue function and solution for K, Kx can be found by iteration. The tax consistent with these solutions can then be derived by using the formulas given above, i.e., Tx, Tx/K.

fee of $3.34 (in 1972 dollars) on each lobster trap fished. This is shown in Table 2. The regulatory authority would collect over $3.5 million in license fee revenue which could be used to finance resource research, enforcement, and surveillance. It should be emphasized that these calculations are merely rough estimates and only serve to give the reader some idea of the magnitude of such license fee. The illustrative license fee is also based upon an extrapolation of trends 5 yr ahead of 1969. If we did nothing, it is estimated that the catch would be lower and more fishermen and traps would be employed in the fishery by 1974. Obviously, the situation would worsen as demand for lobsters expanded and the fishery became increasingly overfished. The license fee plan does have many disadvantages. First, a license fee on traps fished does not really get at the utilization rate. One might expect that a license fee on an individual trap might induce fishermen to fish each trap more intensively and thereby reduce their number of traps. At this point, we do not have any information on utilization rates whereby the tax could be adjusted upward if utilization increased. Second, enforcement and surveillance might be difficult along the coastline from Maine to North Carolina. Third, and most important, the quantitative tools and projected figures needed to calculate a license fee are at best crude and would have to be used for calculations each year.

2. *Reduce the existing level of fishing effort to that necessary to harvest MSY by placing a license fee on traps:* With this scheme, the regulatory authority would calculate a license fee on traps which would reduce the level of existing effort to that necessary to harvest maximum sustainable yield (i.e., estimated to be about 1,011,910 traps) despite an increase in demand for lobsters.[33] Because we are actually reducing fishing effort as opposed to freezing it at the 1969 level, the estimated 1974 license fee per trap must be higher or $5.58 (in 1972 dollars). Actual catch will not be significantly higher. The regulatory authority would receive approximately $5.6 million in license fee revenue. However, this plan has the same disadvantages of a general license fee plan indicated under alternative one.

3. *Reduce the existing level of fishing effort to that necessary to make the marginal cost of*

[33] The fishing effort needed to harvest MSY was obtained from equation (23) with the 1950-69 average water temperature.

TABLE 2.—The impact of various management schemes imposed on the inshore American lobster fishery in 1974.[1]

Economic variables	Estimated values before imposition of management strategies (1969)	Impact after the imposition of selected management strategies for 1974 (1) Freeze at 1969 level of fishing effort	(2) Reduce fishing effort to E_{MAX}	(3) Reduce fishing effort so $MC = P$	(4) Issue "stock certificate" to vessel owner while freezing effort at 1969 level	(5) Do nothing
Catch (million lb)	28.6	28.6	28.7	23.9	28.6	28.1
Value of catch (million $)	28.0	36.8	36.9	31.9	36.8	36.4
Vessels (full-time equivalent)	1,900	1,900	1,798	1,060	1,900	2,070
Traps (million)	1.069	1.069	1.011	0.597	1.069	1.165
Ex-vessel price	0.98	1.29	1.29	1.33	1.29	1.30
Total license fees collected (million $)	0	3.56	5.58	13.3	0	0
License fee/vessel ($)[2]	0	1,877	3,119	12,622	0	0
License fee /trap ($)	0	3.34	5.54	22.43	0	0
Return per vessel and fisherman	6,365	8,400	8,400	8,400	10,278	8,400

[1] Projection of 1974 impact of selected management strategies. Assumes that $F^\circ = 48°$; Y = $677.9 billion, (1969 prices); POP = 212.4 million; $Q_0 + I =$ 183.6 million pounds and $\hat{\pi}$ = $15,292. All prices and dollar values projected for 1974 are expressed in 1972 dollars.

[2] The license fee per vessel was obtained by multiplying the tax per trap by the average number of traps (562.8) fished per full-time vessel.

landings equal to ex-vessel price by placing a license fee on traps: The idea here is to obtain the greatest "net economic benefit" and has been suggested by such economists as Crutchfield and Pontecorvo (1969).[34] If a regulatory authority were to try this for 1974, it would have a drastic impact on the fishery as the number of full-time equivalent vessels and traps would be reduced by approximately 47%. To accomplish this objective an estimated 1974 license fee of $22.43 (in 1972 dollars) per trap would be needed. This would yield the regulatory authority approximately $13.3 million in revenue. From an economic point of view, it is argued that this management strategy will result in the most efficient operation of the fishery if fishermen and vessels can easily move to other fisheries or industries. However, this strategy may be particularly unwise in rural areas such as Maine where labor mobility is low. A drastic cutback in the number of fishermen may create social problems where the cost would greatly exceed any benefits derived from this management strategy. Therefore this management strategy is difficult, if not impossible, to justify on economic grounds for many rural areas where the fishing industry is located and also has the same disadvantages of a general license fee plan on traps as discussed above.

4. *Issue "stock certificates" to each vessel owner based upon average catch over last 5 yr while freezing the existing level of fishing effort:* Under this scheme, the historic rights of each fishing firm would be recognized. In a similar manner to a private land grant procedure, the regulatory authority would simply grant each fisherman a "private" share of an existing resource or catch. The stock certificate would be evidence of private ownership. Individual fishermen would be free to catch up to their allotted share through the use of pots or other biologically permissible technology or, if they desired, trade their stock certificates to others for cash. Suppose the regulatory authority were to freeze the level of fishing effort at the 1969 level and distribute the estimated catch via a stock certificate to the existing fishermen. It should be pointed out that the regulatory authority fixes effort when it selects a given catch. The selected catch could be either MSY or any other level of catch deemed by the regulatory authority not injurious to the viability of the stock. The expansion in demand for lobsters by 1974 would generate excess profits for those individual fishermen who were initially endowed with the property right. By 1974, it is estimated that a full-time lobsterman would be earning $10,278 (in 1972 dollars) a year of which $1,878 would be excess profits (i.e., above opportunity cost). If profits become excessive a license fee would be levied on the fishermen holding stock certificates to insure against increased abnormal returns and provide the regulatory authority with funding to conduct scientific investigations and enforcement. It should be noted that this plan is identical to the license fee scheme which freezes effort at its 1969 level. However, in the latter case, excess profits are taken by the regulatory authority while for this strategy, fishermen are allowed to hold onto the profits generated in the fishery. Since many fisheries are located in rural areas where earnings are traditionally low, this strategy might be justified on the basis that it will raise income levels and thereby help improve living standards to comparable levels to those received in urban areas. This management strategy would, of course, be popular with those already in the fishery. However, new entrants would have to buy stock certificates from those initially in the fishery. This would bring up certain questions of equity and legal precedent which are beyond the scope of this article.

5. *No management strategy:* When considering the economic consequences of alternative management strategies (1-4), it is always wise to assess the results of doing nothing. This gives policymakers a better perspective in evaluating the benefits from taking action. The consequence of doing nothing would be overcapitalization by 1974 with an expansion in the number of full-time equivalent fishermen and traps fished. Approximately 96,000 excess traps (i.e., above that necessary to take MSY) would be in the fishery, and the catch would fall to 28.1 million pounds.

The fishery would grow increasingly overcapitalized, and the resource would be greatly overexploited as demand increased for lobsters during the 1970's. On economic grounds, these

[34] When price is constant, maximization of net economic benefit becomes identical to the goal of maximization of rent to the fishery. This, however, is not the case when the normally downward sloping demand curve is specified.

results are hardly acceptable because more fishermen and vessels will probably be catching less.

6. *Other suggested management strategies:* Reeves (1969) has proposed a hike in license fees to eliminate the marginal or part-time fishermen. He suggests that the present $10 yearly fee in Maine be raised $10 a year over the next 9 yr to a top of $100. In 1969, a little less than one-half of the lobster fishermen were part-time. A part-time lobster fisherman is defined as one who gains less than one-half of his annual income from lobstering. The first step in most suggested limited entry schemes is usually to restrict the fishery to full-time utilization of capital and labor. Two problems occur with this policy. First, the part-time fishermen may represent the most efficient way of taking the catch. If so, the full-time fishermen may be eliminated by increased license fees. Second, license fees do not directly control fishing effort since fishermen may fish more traps. However, Reeves also goes on to argue strongly for limiting the number of traps each fisherman is allowed to set. It is not quite clear whether anyone knows the optimum number of traps per vessel.

Rutherford, Wilder, and Frick (1967) in their study of the Canadian inshore lobster fishery endorse the system suggested by Sinclair (1960). They state:

> "An alternative management system is that suggested by Sinclair (1960) for the salmon fisheries of the Pacific Coast. This would use the licensing of fishermen to limit entry into the fishery. In the first stage, lasting about five years, licenses would be reissued at a fee but no new entries would be licensed, and it would be hoped that during the period there would take place a reduction in the labour and capital input, to take the maximum sustainable catch of salmon at a considerably lower cost. After the end of the first stage, licenses would be issued by the government under competitive bidding and only in sufficient numbers to approximate the most efficient scale of effort; the more competent fishermen would be able to offer the highest bids and it would be expected that the auction would recapture for the public purse a large portion of the rent from the fisheries that would otherwise accrue to the fishing enterprises under the more efficient production conditions in the fishery.
>
> "An arbitrary reduction in the number of fishermen by restriction of licenses to a specified number would entail injustice and inequity as well as grave administrative problems in determining who should be allowed to continue fishing. The auctioning of licenses to exploit a public property resource is justifiable in a private enterprise system of production, particularly when the state is incurring heavy expense to administer and conserve the resource; the recovery by the state of some part of the net economic yield by means of a tax on fishermen (or on the catch) would recoup at least part of such public expenditures, or could be used to assist former fishermen (see strategies discussed above) for instance, by buying their redundant equipment. A tax on fishermen through the auctioning of licenses has, at least, the merit of using economic means instead of arbitrary regulations to achieve a desired economic objective—the limitation of fishing effort to increase the net economic yield from the fishery. Regulations have to be enforced, usually at considerable cost, but economic sanctions tend to be, if not impartial, at least impersonal and automatic in their operation."

Actually, this latter management scheme is similar to the taxing scheme, but uses an auction rather than a direct tax.

Conclusions

The purpose of this article is to explain the use of bioeconomic models in assessing alternative management strategies. For this purpose the data are less than optimal. However, this does not mean that we cannot take steps in the direction of fishery management. In fact, these steps must be taken to protect the resource from destruction and to achieve a better use of vessels and fishermen. It is hoped that the following conclusions will provide a helpful framework in which to consider the merits of limited entry:

1. For the inshore American lobster resource, there is every indication that the fishery has achieved maximum sustainable yield and is fully capitalized. This has been brought about by a rapid expansion in effort (i.e., traps fished) produced by (1) free access to the resource, (2) a rising market for lobsters of all species, and (3) a secular decline in seawater temperature.

2. We have presented the bioeconomic impact of alternative management strategies to both conserve the resource and use it efficiently. The choice of which strategy to pursue is in the public domain and beyond the scope of this paper. However, the economic alternatives are pointed out.

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APPENDIX TABLE—Economic variables associated with the U.S. inshore American lobster fishery, 1950-69.

Year	Catch by traps	Value	Traps fished	Catch per trap	Ex-vessel price	Ex-vessel price divided by consumer price index	Year	Per capita consumption of lobsters	Per capita disposable personal income divided by consumer price index	Consumer price index (1967 = 100)	Mean annual seawater temperature at Boothbay Harbor, Maine
	Thousand pounds	*Thousand dollars*	*Number*	*Pounds*	*Cents per pound*	*Cents per pound*		*Pounds (live weight)*	*Dollars*		*Degrees Fahrenheit*
1950	22,914	8,283	578,930	39.6	36.1	50.1	1950	0.585	1,892	72.1	49.3
1951	25,749	9,328	512,812	50.2	36.2	46.6	1951	.651	1,888	77.8	51.4
1952	24,681	10,469	544,730	45.3	42.4	53.4	1952	.638	1,909	79.5	50.2
1953	27,509	10,687	569,081	48.3	38.8	48.5	1953	.710	1,976	80.1	52.0
1954	26,628	10,250	628,209	42.4	38.5	47.8	1954	.690	1,969	80.5	50.3
1955	27,886	11,003	669,229	41.7	39.5	49.2	1955	.734	2,077	80.2	50.0
1956	25,386	11,584	666,887	38.1	45.6	56.1	1956	.704	2,141	81.4	48.6
1957	29,358	11,263	688,815	42.6	38.4	45.6	1957	.806	2,136	84.3	48.8
1958	26,143	12,890	753,503	34.7	49.3	56.9	1958	.736	2,114	86.6	47.4
1959	27,752	14,043	856,794	32.4	50.6	58.0	1959	.763	2,182	87.3	47.0
1960	29,345	13,657	844,110	34.8	46.5	52.5	1960	.830	2,185	88.7	47.9
1961	25,621	13,662	895,098	28.6	53.3	59.5	1961	.810	2,214	89.6	47.3
1962	26,728	13,770	909,318	29.4	51.5	56.9	1962	.855	2,280	90.6	46.6
1963	27,210	15,299	866,900	31.4	56.2	61.3	1963	.938	2,333	91.7	47.9
1964	26,844	17,689	904,233	29.7	65.9	70.9	1964	.935	2,459	92.9	46.9
1965	24,737	18,764	949,045	26.1	75.9	80.3	1965	.884	2,578	94.5	45.8
1966	25,606	19,517	947,113	27.0	76.2	78.4	1966	.873	2,680	97.2	45.7
1967	22,098	18,162	907,956	24.3	82.2	82.2	1967	.882	2,751	100.0	45.1
1968	26,918	20,648	966,335	27.9	76.7	73.6	1968	.960	2,827	104.2	46.6
1969	26,930	22,997	1,061,807	25.4	85.4	77.8	1969	.999	2,851	109.8	48.0

Source: Fishery Statistics of the United States, various years, U.S. Department of Commerce, Bureau of Labor Statistics, and Robert Dow.

DAILY ACTIVITY, MOVEMENTS, FEEDING, AND SEASONAL OCCURRENCE IN THE TAUTOG, *TAUTOGA ONITIS*[1]

BORI L. OLLA, ALLEN J. BEJDA, AND A. DALE MARTIN[2]

ABSTRACT

Observations were made on the activity and movements of adult tautog, *Tautoga onitis*, in their natural habitat using scuba and by monitoring the movements of individual fish by ultrasonic tracking. Results showed tautog to be active during the day and inactive at night. Fish larger than 30 cm moved out from the night resting place (home site) each day to feed, while younger fish (≤25 cm) remained and fed in close proximity to the home site. Examination of digestive tracts from various-sized fish showed the blue mussel, *Mytilus edulis*, to be the principal food for this population. While older fish appeared to move offshore for the winter, the younger fish remained inshore, wintering over in a torpid state. The significance of the tautog's differential responsiveness, food habits, and daily and seasonal movements are discussed.

The tautog, *Tautoga onitis* (L.), an inhabitant of the western Atlantic, ranges from Nova Scotia to South Carolina, being most abundant between Cape Cod and the Delaware Capes (Bigelow and Schroeder, 1953:478-484). Its distribution is limited primarily to inshore regions with individual populations being highly localized (Cooper, 1966). This fish lives in close association with rocky places, wrecks, pilings, jetties, or almost any bottom discontinuity and for part of its range, is a prominent member of inshore benthic communities. Unlike the majority of labrids, this species is valued as a game fish and is an excellent table fish.

Our aim in this work was to observe and describe the behavior of adult tautog in situ and to relate our findings to the animal's life habits and history. Our queries primarily concerned daily activity and movements, feeding, and seasonal occurrence. The study was carried out on a population residing in Great South Bay, N.Y., using scuba and ultrasonic tracking.

MATERIALS AND METHODS

The study area was along the south shore of Great South Bay, Long Island, N.Y., extending east from the Fire Island Inlet Bridge to 2 km east of the Fire Island Light (Figure 1). Water depth in the study area ranged from 2.4 to 8.8 m with the bottom composed primarily of sand, gravel, and shell.

Two methods were employed to observe the activity and movements of the fish: (1) ultrasonic tracking of a single fish and (2) direct underwater observations while using scuba.

Twelve fish were tracked at different times from August through September 1971 and June through October 1972 (Table 1). Fish were captured at night within the Fire Island Coast Guard basin by a scuba diver using a hand-held net, and each fish was held in a floating cage for periods ranging from 10 to 108 h before a transmitter was attached.

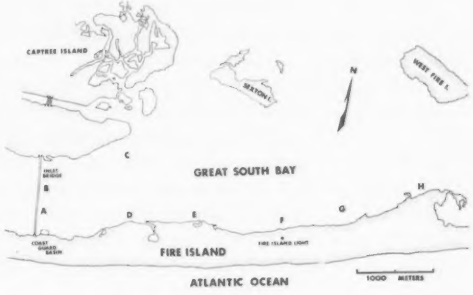

FIGURE 1.—Study area and areas (A-H) of tautog movement as presented in Table 1.

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TABLE 1.—Locations and duration of stay (h) of individual tautog during their daily movements as determined by ultrasonic tracking.

Tautog no.			Day				Night		
			1	2	3	4	1	2	3
1	TL (cm)	45	A3[1](5.0)[2]	A1(2.2)	A4(9.8)	A4(2.6)	A1(11.4)	A1(10.0)	A1(14.1)
	Age[3]/sex	12/♀		A3(10.2)					
	Release (date/time)	7-25-72/1310		A4(1.9)					
	Track duration (h)	67.5							
	Mean temperature	19.2°C							
2	TL (cm)	42	A1(0.8)	A4(11.5)	A3(3.1)	A4(0.5)	A1(9.6)	A1(9.8)	A1(9.6)
	Age/sex	10/♀	A4(0.4)	A5(2.3)	A4(9.2)				
	Release (date/time)	8-1-72/0940	C (8.4)		A5(1.8)				
	Track duration (h)	68.3							
	Mean temperature	21.2°C							
3	TL (cm)	42	A1(3.0)	A4(0.9)	A5(6.2)	A5(0.3)	A1(11.3)	A1(11.6)	A1(10.8)
	Age/sex	10/♀	A4(3.0)	A9(10.3)	A9(7.0)				
	Release (date/time)	8-8-72/1215							
	Track duration (h)	66.5							
	Mean temperature	20.4°C							
4	TL (cm)	43	A1(1.0)	A3(2.5)	A4(0.5)		A1(12.8)	A1(15.6)	
	Age/sex	9/♂	A4(5.7)	A5(0.8)					
	Release (date/time)	9-15-71/0830	A6(0.6)	A6(4.5)					
	Track duration (h)	47.5	A7(2.3)	A7(0.8)					
	Mean temperature	22.0°C							
5	TL (cm)	38	A1(0.3)	A5(2.7)	A5(1.0)		A1(16.6)	A1(15.1)	
	Age/sex	7/♀	A4(0.2)	A6(1.4)					
	Release (date/time)	9-27-71/1400		A7(4.0)					
	Track duration (h)	41.5		A8(0.1)					
	Mean temperature	18.1°C							
6	TL (cm)	47	A1(1.4)	A2(10.9)	F (4.1)		A1(10.3)	G (12.2)	
	Age/sex	11/♂	A5(0.3)						
	Release (date/time)	8-16-71/1830							
	Track duration (h)	41.5							
	Mean temperature	21.7°C							
7	TL (cm)	20	A1(9.4)	A1(12.5)			A1(11.5)	A1(0.6)	
	Age/sex	3/♀							
	Release (date/time)	10-4-72/0930							
	Track duration (h)	34.0							
	Mean temperature	16.8°C							

The transmitter emitted pulsed signals at 70 kHz (kilohertz). Those used for small fish (20-25 cm) measured 30 × 9 mm (manufactured by Chipman Instruments[3]). Larger transmitters, 65 × 14 mm (SR-69B, Smith-Root Inc.) were used for the remaining fish (38-50 cm).

The pharyngeal mill apparatus of the fish precluded internal insertion of the transmitter. This necessitated external attachment through the dorsal musculature, with nylon monofilament line just below the midpoint of the dorsal fin. On each side of the body, rubber disks (25-mm diameter) were used to prevent the flesh from tearing. Tags were made neutrally buoyant by the addition of a styrofoam collar coated with silicone sealant. Following attachment of the transmitter, fish were held in a 50-liter tank for 15 to 30 min to insure that the fish were responsive and that the transmitter was operating normally.

Fish were released within the basin and tracked from a 5.2-m skiff. The signal was monitored with hydrophone and sonic receiver (Model SR-70-H and TA-60 respectively, Smith-Root Inc.) in a manner similar to that described by McCleave and Horrall (1970).

The location of each fish was recorded in relation to local landmarks. We considered a fish active whenever a change in transmitter signal was detected. Direct underwater observations confirmed that we were able to detect abrupt changes in the fish's orientation and straight line movement over 1 m. The data were subsequently condensed to indicate the presence of a fish for a period of time at a specific location (Table 1).

For each track, we recorded current velocity,

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

TABLE 1.—Locations and duration of stay (h) of individual tautog during their daily movements as determined by ultrasonic tracking, continued.

Tautog no.		Day				Night		
		1	2	3	4	1	2	3
8 TL (cm)	25	A1(7.7)	A1(12.5)	A1(12.5)	A1(0.6)	A1(11.4)	A1(11.5)	A1(11.5)
Age/sex	4/♀							
Release (date/time)	10-3-72/1115							
Track duration (h)	67.7							
Mean temperature	16.8°C							
9 TL (cm)	50	D (0.5)	D (10.1)	D (4.9)		G (8.0)	D (7.9)	
Age/sex	14/♂	E (10.9)	E (3.0)					
Release (date/time)	6-14-72/0855		F (0.6)					
Track duration (h)	48.8							
Mean temperature	14.1°C							
Renewed track		D (3.9)	D (16.8)	D (10.2)		D (7.9)	D (7.9)	
Date/time	6-19-72/1750			E (3.1)				
Track duration (h)	49.9							
Mean temperature	15.5°C							
10 TL (cm)	43	A5(8.6)	A5(9.8)			A5(10.2)	A5(8.3)	
Age/sex	9/♂		A6(5.6)					
Release (date/time)	6-27-72/1025							
Track duration (h)	42.5							
Mean temperature	17.3°C							
11 TL (cm)	44	A1(1.1)						
Age/sex	11/♀	A2(1.8)						
Release (date/time)	6-5-72/1345	B (0.6)						
Track duration (h)	3.5							
Mean temperature	13.4°C							
12 TL (cm)	45	A1(0.3)						
Age/sex	12/♀	A5(3.2)						
Release (date/time)	6-12-72/1145	A6(2.7)						
Track duration (h)	8.3	A8(0.3)						
Mean temperature	13.8°C	B (1.1)						
		C (0.7)						

[1] Location as presented in Figures 1 and 2.
[2] Hours given in parentheses.
[3] Age estimated from calculated total lengths by Cooper (1967).

stage of tide, cloud cover, water temperature, and water transparency. Current velocity was measured either with a Beauvert midget current meter or by the float method. The current velocity ranged from 0.65 to 1.75 m/s. Temperature was measured with a thermistor and transparency with a secchi disk. Cloud cover was visually estimated.

In conjunction with our tracking, we directly observed tautog in the study area with scuba for a total of 135 h (90 h daytime and 45 h nighttime).

To identify periods of feeding as well as the types and amounts of food ingested, we examined the digestive tracts of fish collected at different times of the day and night. We measured the relative digestive tract fullness of each volumetrically with the fullness index being the quotient of displacement volume of empty tract/displacement volume of tract with contents.

Determination of the maximum size of mussel that the tautog could ingest and of the maximum size it could crush was made by inserting different size mussels into the mouth and into the anterior opening of the pharyngeal mill. The maximum ingestable size was defined as the largest mussel that could be completely enclosed in the mouth. The maximum crushable size was the largest mussel that could be partially grasped by the pharyngeal teeth.

To aid in describing the method of feeding on mussels, at infrequent intervals over a 16-mo period, we directly observed and used cine analysis of three individuals 25 to 38 cm, held in a 2,200-liter aquarium.

RESULTS

Activity and Movements

The fish which we tracked were active during the day and inactive at night. There was some

degree of variation in the precise time that activity began or ceased relative to morning and evening civil twilight (Table 2). Activity began from 10 min before to 69 min after the start of morning twilight. Cessation of activity, however, was more variable, ranging from 222 min before to 69 min after the end of evening twilight. Although we were unable to arrive at the cause for this variation, there were indications that cloud cover and water transparency, both affecting light penetration, might play a role. Our direct scuba observations (135 h of observation) on untagged tautog showed that the fish were active during the day and inactive at night. Activity as well as responsiveness at night were at such a low level that we were able to touch individual fish or catch them easily with a hand-held net.

Five fish (No. 1-5, Table 1), tracked at different times from July through September 1971 and 1972, exhibited similar patterns in their daily movements. Each morning at the onset of activity or soon after, the fish moved out and usually remained within 500 m of the basin. They spent most of each day at locations in which there were large concentrations of blue mussel (*Mytilus edulis*) (areas A2-A9, Figure 2; Table 1). Towards late afternoon or early evening, the fish returned to the basin and within 1 to 198 min ($\bar{x}=55.7$), settled in one location and remained throughout the night in an inactive state.

Another fish (No. 6, Table 1) tracked during this period returned to the basin the first night after being released, following the same pattern as fishes 1 to 5. However, after spending most of the second day in close proximity to the basin, it did not return but rather, at 172 min prior to the end of evening twilight, swam 6.2 km in a direct easterly course to an artificial reef (consisting of sunken barges and tires) where it spent the night (area G, Figure 1).

Underwater observations made during July through mid-October showed that the number of fish, measuring about 30 to 50 cm, in close proximity to the basin increased just prior to and immediately after the beginning of evening twilight in comparison to the number that were present during the day. Comparing these obser-

TABLE 2.—Onset and end of the daily activity of individual tautog relative to morning and evening civil twilight (MCT and ECT[1]).

	Mean time and range (min) to			
	Onset of activity		End of activity	
Tautog no.	Prior to MCT	Following MCT	Prior to ECT	Following ECT
1		27.0 (21.0 to 35.0)	122.0 (43.0 to 222.0)	
2		20.0 (10.0 to 30.0)	14.7 (8.0 to 26.0)	
3		26.0 (12.0 to 43.0)	71.0 (39.0 to 116.0)	
4	7.0 (4.0 to 10.0)		78.5 (72.0 to 85.0)	
5		23.0 (18.0 to 28.0)	47.5 (12.0 to 83.0)	
6		54.5 (52.0 to 57.0)	28.0 (4.0 to 52.0)	
7		35.0	68.0 (54.0 to 82.0)	
8		27.0 (13.0 to 45.0)	75.3 (51.0 to 88.0)	
9		62.0 (49.0 to 69.0)	131.0 (26.0 to 158.0)	69.0
10		14.0	51.0 (28.0 to 74.0)	

[1] MCT: start of morning civil twilight.
ECT: end of evening civil twilight.

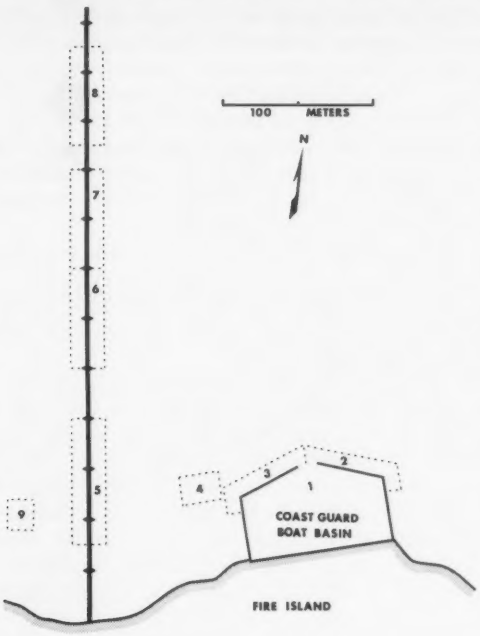

FIGURE 2.—Areas demarcating the locations of tautog during their daily movements as presented in Table 1 (an enlargement of area A, Figure 1).

vations with our tracks of similar-sized fish, we were led to conclude that this increase was the result of the normal nightly return to the basin. However the number of smaller fish ($\leq$25 cm) appeared to remain the same throughout the day and during evening twilight, i.e., there was no discernible increase at evening twilight. To affirm whether the smaller, younger fish did in fact remain closer to the basin during the day than the larger, older ones, we tagged two fish 20 and 25 cm (No. 7 and 8, Table 1), tracking one for 34 and the other for 66.8 h. These fish exhibited the typical habit of the larger fish of being active during the day and inactive at night (Table 2). However, in contrast to the larger fish, these smaller fish remained within the basin and never ventured farther than 2 m from the walls. Examination of the digestive tract of one of these smaller fish, recaptured after tracking had been terminated, showed the presence of mussels throughout the tract, indicating that this fish had been feeding on mussels attached to the basin walls or other substrate within the basin.

These data indicate that tautog occur as an essentially localized population at least from July through mid-October. The basin acts as a focal point for the population, providing a suitable night habitat for all fish and a forage area for smaller fish.

Four fish (No. 9-12, Table 1) tracked during June 1972 exhibited quite different patterns of daily movements. Two of these (No. 9 and 10) ranged farther during the day and spent the night at various locations other than the basin. Tracking was discontinued on the other two fish of this group (No. 11 and 12) during the first day due to inclement weather. However, a search the night following tracking termination and on three successive nights failed to detect the presence of either fish in or around the basin. They, too, evidently spent the night at other locations.

The major difference in fish tracked during June from all other fish tracked was that all June fish were in spawning condition, readily extruding sperm or ova during the tagging procedure. Further, if this population bears any similarities to the Narragansett Bay population (Cooper, 1966), we surmise that during June, fish are still arriving inshore from their offshore wintering area and have not yet become localized (at least fish of the size we were tracking).

On 26 September 1972, during the day, we sighted just outside the basin (Area 3, Figure 2) a tautog with a transmitter attached. Although we could not ascertain when this fish was tagged, it had been 49 days since the last tagging. The fish, which appeared normally responsive, had either remained localized within this area for at least 49 days or possibly was one of the four fish tagged during June that had not returned to the basin at that time.

Feeding

There were varying amounts of food throughout the digestive tracts of fish sampled at various times of the day and just after evening twilight (Table 3). The tracts of fish sampled just prior to morning twilight (23-83 min), while still in an inactive night condition, were empty. Thus it appears that the fish feed throughout the day, beginning soon after morning twilight and continuing up to evening twilight. Assuming that the fish sampled just before morning

twilight had fed up to the previous evening twilight, passage through the digestive tract while the animals were quiescent took 8 h or less.

Examination of the matter ingested showed that 70% of the fish sampled contained 78.4 to 100% mussels, by volume, in various stages of digestion (Table 3). Next in abundance were remains of various decapod and cirriped crustaceans, followed by an assortment of other invertebrates and debris (vegetable matter, sand, and gravel), with some of the latter probably being ingested incidentally with the mussels. All but two of the fish examined contained over 50% mussels, by volume, indicating that mussels are the principal food for this population.

Observations on the tautog's method of feeding on mussels, in both the field and laboratory, revealed that after approaching a clump of mussels, the fish would grasp one or several at a time with the anterior canine teeth and then tear them from the substrate with an intense lateral or shaking movement of the head. In no case, in either the field or laboratory, did the initial ingestion process involve crushing with the canines. After initial ingestion, muscular contractions in the bucco-pharyngeal area were clearly seen, evidentally resulting from the shells being crushed by the pharyngeal teeth. When a clump of mussels attached by byssal threads was too large to be processed by the pharyngeal teeth, the fish would alternately ingest and egest the clump until it was separated into a smaller crushable size.

The mussels in the digestive tracts consisted primarily of specimens averaging 11.9 mm in length and estimated to be 1 to 2 yr old (Table 3). There was an obvious selection of young, small mussels by all-sized fish.

While factors such as ease of crushing and a greater digestive efficiency may be involved in the tautog's preference for small, young mussels, we found another possible cause related to the limitations imposed by the dimensions of the pharyngeal area where the mussels are crushed. The mouth can accommodate much larger mussels than the crushing apparatus is able to process. For example in the laboratory on 20 occasions, we saw fish that were starved for more than a day attempting to eat mussels

TABLE 3.—Relative fullness and contents of tautog digestive tracts.

Time of capture (EDT)	Fish length (cm)	Fullness index[1]	% of total gut contents			Median length of mussels (mm)	% of mussels less than 30 mm
			Mussels	Decapod and cirriped crustaceans	Other		
0400-0500	23.5	1.0					
	23.5	1.0					
	45.0	1.0					
	37.0	1.0					
	46.0	1.0					
0800-0830	24.0	0.8	85.7	5.8	8.5	14	100.0
	27.5	0.7	100.0			12	100.0
	26.5	0.7	99.5		0.5	14	100.0
	34.0	0.8	62.5		37.5	16	100.0
1200-1300	31.0	0.6	89.6	4.5	5.9	15	100.0
	36.5	0.5	65.3	27.0	7.7	8	100.0
	37.5	0.6	78.5	16.1	5.4	16	100.0
	21.0	0.7	98.6		1.4	11	100.0
	24.5	0.7	100.0			5	100.0
	32.0	0.4	95.2	4.8		15	100.0
	29.0	0.4	54.5	36.4	9.1	10	100.0
1600-1700	40.0	0.7	99.1	0.6	0.3	8	100.0
	32.0	0.4	92.2	6.0	1.8	8	100.0
	32.5	0.6	31.3	68.1	0.6	8	100.0
1930-2000	44.0	0.4	90.4	9.6		14	88.1
	36.0	0.6	45.9	41.3	12.8	12	87.5
	46.0	0.6	65.7	32.9	1.4	10	53.8
	37.0	0.6	92.3	7.7		15	100.0
	42.5	0.4	94.0	6.0		16	72.7
	[2]20.0	0.6	78.4		21.6	11	100.0

[1] Fullness index = volume empty tract/volume of tract with contents.
[2] Fish no. 7 (Table 1) captured at end of track.

larger than could be crushed by the pharyngeal teeth. The fish would ingest the mussel, unsuccessfully attempt to crush it, and then egest it, the process being repeated 20 to 30 times. We also found in a preliminary determination of the maximum crushable size that fish, 34 to 53 cm, could crush mussels that were only 0.47 times the maximum size they could ingest.

Seasonal Movements

Direct observations made during the day with scuba from October 1971 through May 1972 and from October 1972 through January 1973 indicated that there was a difference in the seasonal movement between small fish ($\leq$25 cm, 2-3 yr old) and large fish (>25 cm, >4 yr old). The ages of fish were estimated from calculated total lengths by Cooper (1967). Tautog of varying sizes were observed in close proximity to the basin on 12 October 1971, at an average water temperature of 17.0°C (range: 15.2°-19.5°C). On 1 November with the water temperature averaging 10.0°C (range: 8.9°-10.6°C), no large tautog were sighted, but about 25 small ones were seen swimming within 1 m of the basin walls. Small fish were still active on 18 November (water temperature 10.0°C: 9.7°-10.1°C). On 9 December 1971, and 5 January 1972, with temperatures ranging from 4.0° to 5.5°C, a total of approximately 40 small tautog was sighted within the basin. These fish appeared lethargic and rested against the basin walls. When prodded by a diver, they moved only a few feet before settling to the bottom once again.

Both large and small fish were sighted on 10 May 1972 with an average temperature of 10.0°C (range: 8.5°-11.5°C) and appeared normally active.

Diving observations the following fall and winter substantially supported the fact that small fish wintered inshore. On 2 October 1972, we sighted normally active large and small tautog (water temperature 16.8°C: 16.2°-17.7°C). On 26 October with the temperature averaging 10.0°C (range: 9.6°-10.5°C), we found no large fish but sighted at least 30 small fish which appeared normally active. During dives on 27 November and 29 December 1972, and 9 January 1973, with the temperature ranging 2.0° to 4.8°C, we sighted approximately 35 small fish ($\leq$ 25 cm) lying in a torpid state on the bottom between pilings and the basin walls or in bottom depressions within 10 cm of the wall. Some of these fish were partially covered with silt. Opercular movements were so shallow as to be almost undiscernible. Examination of the digestive tracts of five fish captured during this period showed that the fish had not eaten for some time as indicated by the empty and flaccid condition of the tracts.

We concluded from these observations that fish at least larger than 25 cm moved offshore to winter, agreeing with the conclusions of Cooper (1966) for a population residing in Narragansett Bay, Rhode Island. However, small fish (approximately $\leq$25 cm) remained inshore throughout the year in close proximity to the home site.

DISCUSSION

The tautog's pattern of being active during the day and inactive at night is a typical labrid trait having been observed in a number of species. For example, field observations in the Pacific by Hobson (1965, 1968, 1972) showed this pattern to be present in five species (*Bodianus diplotaenia, Halichoeres nicholsi, Labroides phthirophagus, Thalassoma duperrey,* and *T. lucasanum).* The pattern was presumed to be present in *Halichoeres dispilus, Hemipteronotus mundiceps,* and *H. pavoninus* since the fish were observed in the active state during the day but not sighted at night, having apparently buried under sand or rested in crevices. Field observations in the Atlantic by Starck and Davis (1966) on *Bodianus rufus, Clepticus parrai, Lachnolaimus maximus,* and *Thalassoma bifasciatum* also show the typical labrid day active/night inactive pattern.

Whether a labrid species spends the night buried under sand or lying in cracks or crevices, all appear to be in a state of low responsiveness. Tauber and Weitzman (1969) investigated the level of responsiveness of the slippery dick, *Irideo bivittata,* at night. They found the fish to be in a state that resembled the mammalian sleep phase characterized by decreased responsiveness to altering stimuli, diminished or irregular respiration, and eye movement activity.

The low level of responsiveness present at night in labrids and other species with a similar habit has wide ramifications with regard to

susceptibility to environmental stress. The probability that fish would be able to respond and escape potentially lethal environmental perturbations during the inactive night phase would be less than if the same stress were applied during the day. Physiological responses would also differ. Differential susceptibility to stresses as related to the daily rhythm has been clearly established (for discussion and review, see Reinberg, 1967).

During most of the summer and into early fall, fish of the colony we studied had a fairly well defined home range (Gerking, 1959) with the basin acting as a focal point or home site, providing a suitable night habitat for all-sized fish. While larger fish ($\geq$30 cm) moved out each day to feed, the smaller fish ($\leq$25 cm) foraged along or in close proximity to the basin walls. The adaptation of young fish remaining close to the home site may relate to effectively protecting them against predators. On one occasion while diving in early July 1972, we observed three striped bass (*Morone saxatilis*, 80-90 cm) actively pursuing and attempting to capture young tautog ($\leq$25 cm) from a group of 30 to 40. The tautog were within 1 m of the basin wall at the onset of the attack. They escaped from the predators by swimming directly to the wall where they remained in crevices. The older fish, not as susceptible to predation, moves out to feed, resulting in a fuller utilization of the potential energy resources of the area and in the probable reduction of feeding competition among individuals. The reduction in the probability of feeding competition seemed especially critical since all sizes studied preferred, to a large extent, similar-sized mussels. This daily movement of the larger fish out of the basin also seemed to make the home site a nursery for young fish.

Our observations that tautog larger than 30 cm (approximately 5 yr or older) were not present in the vicinity of the basin after the end of October circumstantially agree with the finding of Cooper (1966) that Narragansett Bay fish of similar size wintered offshore. In contrast, our results showed that younger fish remained inshore throughout the year, wintering at the home site in a torpid, nonfeeding state. It is apparent that the younger fish are highly dependent on the home site throughout the year for at least the first 3 to 4 and perhaps 5 yr of their life. The habit of remaining inshore over the winter is not unknown in labrids. Green and Farwell (1971) found various-sized cunner, *Tautogolabrus adspersus*, lying in a torpid state inshore when temperatures fell below 5°C.

Although tautog feed readily on other types of food, the most abundant food available and found most frequently in the digestive tract was mussels. Mussels were predominantly less than 30 mm long, indicating an average age of 1 to 2 yr (Savage, 1956). The next most abundant food found in the digestive tract was various crustaceans, with only negligible amounts of other items. It seemed that, on the basis of our diving observations, the crustacean population, in terms of a potential alternate food source for the tautog in this area, did not approach the abundance of mussels in the 1 to 2 yr class. We surmise that the equilibrium of the population, in terms of food resources, is highly dependent on a single food item, with no alternate potentially serving as a sustaining element.

Environmental perturbations that would directly affect 1- to 2-yr-old mussels or any of the pre-adult stages, would lead to a high probability of stress in the tautog population. This would be especially true for young fish (3 yr or less) since they seem especially dependent upon the home site. This dependence on the home site raises the question of whether or not it is within their capability to move out and seek new feeding areas and if so, how successful would they be.

Another obvious limiting element of the population is a suitable physical structure which all-sized tautog require during their night inactive phase and upon which young tautog seem totally dependent. In areas where food resources are in relative abundance to support a population, the introduction of a suitable physical habitat could lead to the establishment of new discrete colonies.

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AN EXAMINATION OF THE YIELD PER RECRUIT BASIS FOR A MINIMUM SIZE REGULATION FOR ATLANTIC YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

Some of the conceptual foundations of yield-per-recruit analysis as a management tool and as applied to the Atlantic yellowfin tuna fishery were critically explored. Problems examined include: (1) estimating the current state of the fishery in terms of a knife-edged recruitment approximation, (2) inferring consequences of management action from the yield-per-recruit isopleth, (3) the difficulty in achieving a maximum yield per recruit when there exist several gear types exploiting different size ranges, (4) the difficulty in obtaining projected increases in yield per recruit when the killing and discarding (dumping) of fish smaller than the optimum size occurs, and (5) the possible interaction between a size limit and the projection of the maximum sustainable yield.

In employing yield-per-recruit analysis to the Atlantic yellowfin tuna fishery, two approaches were taken—one approach makes use of a wide range of parameter estimates and a number of simplifying assumptions, but little data, and the other approach makes use of considerably more data, but is more confined in the parameter estimates and uses fewer of the simplifying assumptions. The general results of both approaches, assuming no dumping occurs, indicate that only minor increases in yield per recruit would occur if the size at recruitment is increased from our estimate of the present size at recruitment and fishing effort remains constant; an increase in fishing effort without changing other aspects of the fishery would not appreciably increase yield per recruit; and an increase in size at recruitment and in fishing effort would result in modest gains in yield per recruit. Specifically meeting the request of the International Commission for the Conservation of Atlantic Tunas, we recommended that a minimum size limit regulation in the vicinity of 55 cm (3.2 kg) be enacted.

The second regular meeting, in Madrid, Spain, on 2-7 December 1971, of the commission of ICCAT (International Commission for the Conservation of Atlantic Tunas) authorized the "Council to recommend to the Contracting Parties that they prohibit landing of yellowfin weighing less than a minimum weight somewhere between 3.2 and 10 kg." This recommendation was based on studies by members of the Subcommittee on Stock Assessment that showed that theoretically the size at first capture which maximizes the yield per recruit of yellowfin is between 10 and 25 kg.

A special ICCAT working group on stock assessment of yellowfin tuna met in Abidjan, Ivory Coast, 12-16 June 1972, to consider further scientific aspects of size regulation and other matters pertaining to the Atlantic yellowfin fishery (ICCAT, 1972).[2] Studies on yield per recruit were presented by Hayasi, Honma, and Suzuki (1972);[3] Joseph and Tomlinson (1972);[4] and Lenarz and Sakagawa (1972).[5] A similar study was published by Wise (1972)

[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, LaJolla, CA 92037.

[2] ICCAT. 1972. Report of the meeting of the special working group on stock assessment of yellowfin tuna (Abidjan, June 12-16, 1972). Manuscript on file at ICCAT General Mola 17, Madrid, 1 Spain.

[3] Hayasi, S., M. Honma, and Z. Suzuki. 1972. A comment to rational utilization of yellowfin tuna and albacore stocks in the Atlantic Ocean. Far Seas Fisheries Research Laboratory, Orido 1000, Shimizu, Japan. Unpublished manuscript.

[4] Joseph, J., and P. K. Tomlinson. 1972. An evaluation of minimum size limits for Atlantic yellowfin. Inter-American Tropical Tuna Commission, La Jolla, Calif. Unpublished manuscript.

[5] Lenarz, W., and G. Sakagawa. 1972. A review of the yellowfin fishery of the Atlantic Ocean. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

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before the meeting. The report of the meeting may be considered as a summary of these papers, which indicated that increases in size at recruitment would probably increase yield per recruit but not by more than about 10%.

The special ICCAT working group also examined available evidence on the practicability of minimum size regulations. Scientists of the group were concerned that since the gears that fish for yellowfin in the Atlantic supposedly kill most fish that are captured, a minimum size regulation would reduce the number of small yellowfin that are landed but would not have the desired effect of reducing mortality rates of small yellowfin. This, of course, assumes that schools of yellowfin containing yellowfin less than any minimum size would actually be set upon. In this connection the group noted that the conditions which must be met before minimum size regulations can be effective are: (1) the fishermen must be able to estimate the size of yellowfin in a school, and (2) there must be little or no mixing of small yellowfin with large yellowfin within schools.

Very little evidence is available from the Atlantic on these subjects. Ten samples were presented at the Abidjan meeting that indicated considerable mixing of small yellowfin (<5 kg) with large yellowfin (>5 kg) within schools. The working group also took note of a study on the subject by Calkins (1965) when size regulations were being considered by the IATTC (Inter-American Tropical Tuna Commission) for the yellowfin fishery in the eastern tropical Pacific. Calkins, working with only one hypothetical minimum size out of a range of 12.7 to 25.0 kg, concluded that a 12.7-kg size regulation would be seriously complicated by size variation within sets. He also noted that a considerable amount of small yellowfin are often captured in sets that include skipjack. Thus it appears that it would not be possible to fish for skipjack without killing some small yellowfin. Evidence based on the few samples from the Atlantic indicated that sets would include yellowfin tuna larger and smaller than 5 kg; thus even if a minimum size regulation were set at this value it would be difficult to prevent the capture of fish smaller than 5 kg.

The working group recommended that more data should be collected on the subject from the Atlantic. The working group also noted that a reduction in the size at first recruitment should be prevented and that minimum size regulations of 3.2 kg that have been passed by several African nations should help prevent a reduction in size at recruitment.

The population dynamics of Atlantic yellowfin tuna are complex because the fishery is prosecuted by several types of gear: bait boats, small purse seiners, large purse seiners, and longliners. These gears tend to capture different sizes of fish and thus affect the population in different ways. FAO (1968) noted that longline gear tends to capture large yellowfin while the other gears capture small yellowfin. Lenarz (1970),[6] with more recent data, showed that American[7] purse seine gear tends to capture relatively more large yellowfin—in significant quantities—than was indicated for the earlier surface fishery. Joseph and Tomlinson (1972, see footnote 4) presented data that indicated small purse seiners of France-Ivory Coast-Senegal (FIS) tend to capture relatively more small yellowfin than the large FIS and American purse seiners. The differences among size selectivity of the four gears necessitates consideration of the physical makeup of the fleet when examining size regulations. Therefore, considerable attention was paid to this aspect of the problem during the study.

The above paragraph might be taken to imply that adequate data are available respecting the relative quantities and size distributions of fish caught by the various gears. It is our feeling that the adequacy of the data needs to be demonstrated. We cannot place much faith in the details of the relative size distributions per unit effort among the various fishing units, but we do feel that the general orders of magnitude are essentially correct. We should also point out that with the improvement in data over the last several years, the interpretations which accrue from the data and our appreciation of the considerable complexity of the fishery are more evident.

Definitions of Minimum Size

Because this paper discusses minimum size, it is necessary to define the term explicitly to

[6] Lenarz, W. 1970. Estimates of yield per recruit of Atlantic yellowfin tuna. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

[7] Refers to vessels registered in Canada, Panama, and the U.S.A.

avoid ambiguity and to prevent possible misapplications of the results of this study. "Minimum size" may be viewed from two aspects: absolute minimum size and effective minimum size. Absolute minimum size is defined as the smallest fish in the catch and is related to the concept of knife-edged recruitment in defining the size at recruitment to the fishery. Recruitment is defined as the act of becoming vulnerable to fishing. In the case of knife-edged recruitment, no fish are vulnerable to fishing prior to the size at recruitment. Fish that are larger than the size at recruitment are fully vulnerable to fishing. Since most recruitment is size specific, hence sequential, the term effective minimum size is also needed. Effective minimum size is that size whose corresponding age is used as the lower bound for integration of the yield equation as if recruitment were knife-edged, and which gives the same yield per recruit as the sequential recruitment case.

Approaches to Yield-Per-Recruit Analysis

This paper examined several of the concepts involved in yield-per-recruit analyses because the question of what is the optimum minimum size for a given rate of exploitation is usually interpreted through such analyses. Both the classical approach, in which fishing mortality is constant with knife-edged recruitment, and the more complex approach, in which fishing mortality is size specific, are explored.

Throughout the paper we have intentionally kept mathematical notation to a bare minimum. We believe that most of the equations used are well known to readers actively involved in stock assessment. Readers who are not familiar with the equations can find excellent descriptions in the cited literature.

Employing the classical approach to yield-per-recruit analysis involves: (1) estimating the age or size at recruitment which represents an approximation of the current state of the fishery in terms of knife-edged recruitment; (2) finding the age or size at recruitment which maximizes the yield per recruit at a given level of fishing mortality; (3) imposing some regulation on the fishery such to achieve as its effective minimum size, the age or size at recruitment which maximizes the yield per recruit. The advice from the yield-per-recruit isopleth (in terms of the optimal age or size at recruitment) may be interpreted as either a knife-edged absolute minimum size or as an effective minimum size. Since for the fishery under consideration (and for many other fisheries as well) recruitment is not knife-edged, then we are talking about an effective minimum size. Now, on the other hand, if we assume that the absolute minimum size, the regulated size, and the effective minimum size are all the same, then we will have an inappropriate estimate of the yield per recruit, and the optimum may not be achieved. Somehow we need to determine the relationship between the effective minimum size and the regulated size; in some instances they can roughly be the same; but this equality will usually not obtain if the regulated size is chosen to be the absolute minimum size in the catch.

The more complex approach, which estimates size-specific fishing mortality, circumvents the first difficulty encountered in the classical approach, i.e., determining a knife-edged approximation to the current state of the fishery. The problem still remains, however, as to interpretation of the advice from the yield-per-recruit isopleth in terms of an effective minimum size. Joseph and Tomlinson (1972, see footnote 4) used the more complex approach in a recent study on minimum size regulations for the Atlantic yellowfin fishery. We have updated their analysis by using data made available at the Abidjan meeting and have also examined the sensitivity of the methodology to various sources of errors in the data.

DATA, PARAMETERS, AND COMPUTER PROGRAMS

Data

Catch- and length-frequency data for each type of gear for the 1967-71 period were obtained from the report of the meeting of the special ICCAT working group (Tables 10, 11, and 12 of ICCAT, 1972, see footnote 2) with the exception of length-frequency data of the 1967-68 FIS fishery and 1971 Japanese longline fishery. Length frequencies for the 1967-68 FIS fishery were compiled from various ORSTOM (Office de la Recherche Scientique et Technique Outre-Mer) publications (Lenarz and Sakagawa, 1972, see footnote 5). Length

frequencies from the 1971 Japanese longline fishery are assumed to be the same as those of the 1970 Japanese longline fishery; this assumption appears justifiable because year to year changes in length frequencies from longline fisheries tend to be less than differences in length frequencies between longline fisheries and surface fisheries.

Length-frequency data were available only from the Japanese longline fishery, FIS surface fisheries, and American large purse seine fishery. Thus it was necessary to make several assumptions before estimating the length frequencies of the total catch of yellowfin in the Atlantic. Length frequencies for longline fisheries other than Japan are assumed to be the same as Japan's. Length frequencies for the bait boat and small purse seine fisheries other than FIS were assumed to be the same as the FIS fishery. Length frequencies for the large purse seine fisheries other than FIS and American were assumed to be the same as those two fisheries.

Parameters

The growth equation [$L = 194.8 \times (1 - e^{-0.42(t - 0.62)})$] presented in LeGuen and Sakagawa (1973) and length-weight relationship ($W = 0.0000214L^{2.9736}$) given by Lenarz (1971a)[8] were used, where L is fork length in cm, t is age in years, and W is weight in kg.

The annual instantaneous coefficient of natural mortality (M) is a difficult parameter to estimate and due to a lack of data only preliminary estimates have been made for the parameter in the Atlantic. We assume as most authors have that M is constant over the exploited phase. Estimates of $M = 2.61$ and 1.50 for the Atlantic were made by Pianet and LeHir (1971) based on data from bait boats and seiners, respectively. These estimates seem unreasonably high perhaps because their data were only from the Pointe Noire region which is a small area compared to the total region in the Atlantic where yellowfin tuna are found. Hennemuth (1961) estimated that M is 0.8 in the Pacific while Davidoff (1969) chose the upper bound of Hennemuth's estimate, 1.0. Hennemuth's work was based on estimates of instantaneous coefficient of total mortality (Z) made from age compositions of catches by primarily bait boats and an estimate of instantaneous coefficient of fishing mortality (F) from Schaefer (1957). Since bait boats appear to be selective for small yellowfin, F and Z are not constant, and methods of ageing yellowfin have not been proven correct, Hennemuth's estimate must be considered a first approximation. However, his estimate seems reasonably consistent with what is thought to be the life span of yellowfin. We assumed for the purposes of our calculations here that M is 0.8 as is conventional (based on Hennemuth's work in the Pacific); we also used values of 0.6 and 1.0 to encompass what we believe is the range of reasonable values.

Pianet and LeHir (1971) also estimated an average F of 0.88 for the segment of the Atlantic yellowfin tuna population that is exploited in the Pointe Noire region. As we have indicated, their estimate is not representative for the population as a whole.

Our range of estimates of Z for 1967-71 is 0.91 to 1.82 (Lenarz and Sakagawa, 1972, see footnote 5). If we assume that $M = 0.8$ for the Atlantic population, then F is 0.11 to 1.02. We believe that F is about 0.6 for recent years. However, we used a range of F values in our study.

Computer Programs

Most of the calculations were performed on the Burroughs 6700[9] computer at the University of California at San Diego. Programs used in the analysis, except for FRG708 (Paulik and Bayliff, 1967), were written by the authors; they are as follows:

1. Simplified Beverton and Holt yields per recuit—YPER.
2. Accuracy of knife-edged approximations of age at entry and interactions between minimum size and catch quota regulations—GXPOPS.
3. Yield-per-recruit isopleths under knife-edged recruitment—FRG708.

[8] Lenarz, W. 1971a. Length-weight relations for five Atlantic scombrids. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

[9] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

4. Size-specific rates of fishing mortality—COHORT.

5. Yield-per-recruit isopleths for multigear fisheries with size-specific F—MGEAR.

6. Optimum size at recruitment under different levels of effort by two gears—OPSIZE.

ANALYSIS

As previously mentioned in the introduction, we use two approaches in analyzing the data, the knife-edged recruitment approach and the size-specific F approach.

Knife-Edged Recruitment Approach

Introduction

Two commonly used models for computing yield per recruit and determining the size at recruitment which maximizes yield per recruit are those of Beverton and Holt (1957) and Ricker (1958). We employed both models for knife-edged approximation analyses—the simplified Beverton and Holt model, making use of a wide range of parameter estimates or extrapolations from fisheries for similar species, and the Ricker model, making use of the best parameter estimates and giving a more detailed analysis of yield per recruit. We used the Ricker model instead of the Beverton and Holt model for calculating yield-per-recruit isopleths because the Ricker model allows the use of exponents in the length-weight relationship with values other than 3. It is important to stress that the material in the simplified Beverton and Holt model involves fewer assumptions than the material in subsequent sections. This is important because as our approach becomes more complex the data requirements become more rigorous. It can be argued that we have sufficient data for this simplified approach. In the more complex approaches this assertion becomes more tenuous; because we use more assumptions in the more complex approaches we do not necessarily obtain more information, even though it may appear that way. However, it should be noted that the assumption of a constant rate of mortality over the fishable life span contained in the simplified approach may be important, and we believe that it is not fulfilled. These analyses are followed by sections discussing the problems of determining the proper parameters which represent the current situation of the fishery.

Simplified Beverton and Holt Model

The Beverton and Holt yield-per-recruit model may be simplified such that relative yield per recruit, Y', is a function of three ratios:

$$C = l_r'/L_\infty$$
$$Q = M/K$$
$$E = F/(F + M)$$
$$Y' = Y/(RW_\infty)$$

and where l_r' is the size (length) at recruitment, W_∞, L_∞, and K are parameters of the von Bertalanffy growth equation, Y is yield in weight, and R is recruitment. Y' is tabulated in Beverton and Holt (1966), but more extensive calculations were performed with program YPER.[10] Beverton and Holt (1959) concluded that, within reason, there exists a common ratio between M and K within related species groups. Therefore, a range of estimates for the various parameters is utilized along with other information obtained by examining parameter estimates for M and K for yellowfin tuna from areas other than the Atlantic.

The range of values for the various parameters is as follows: $K = 0.28$ to 0.53 and $L_\infty = 175.2$ to 223.0 cm from LeGuen and Sakagawa (1973), $Z = 0.91$ to 1.82 from Lenarz and Sakagawa (1972, see footnote 5), and $M = 0.6$ to 1.0. From these ranges of estimates, a maximum range for E is 0.0 to 0.67 and for Q is 1.13 to 3.57. Using our most reasonable parameter estimates of $K = 0.42$, $M = 0.8$, and $Z = 1.4$, however, a reasonable range for E and Q was established by allowing either the numerator or denominator of the ratio to be one of our most reasonable estimates—the reasonable ranges are $E = 0.12$ to 0.56 and $Q = 1.42$ to 2.86. With $K = 0.42$, $M = 0.8$, and $Z = 1.4$, our most reasonable estimates of E and Q are 0.43 and 1.9, respectively.

Table 1 contains optimal values of size (cm) at recruitment, $l_r^{*\prime}$, for the maximum range of estimates of E and Q (deleting the impossible $E = 0.0$) for the range and most reasonable estimates of L_∞. The dashed lines enclose the

[10] For some values of c, Table IIb of Beverton and Holt (1966) was slightly higher than computed by YPER; this may be due to differing methods of rounding.

Table 1.—Optimal values of size at recruitment (cm) as a function of the rate of exploitation (E) and the ratio of M to K (Q) for three estimates of L_∞.[1]

	E						
Q	0.1	0.2	0.3	0.4	0.5	0.6	0.7
			L_∞ = 175.2 cm				
1.0	56.6	73.1	84.4	94.3	102.3	109.5	115.8
1.5	49.4	64.1	74.8	83.4	90.8	97.1	102.8
2.0	43.8	57.1	66.9	74.8	81.5	87.2	92.5
2.5	39.4	51.7	60.4	67.8	73.9	79.4	84.1
3.0	35.9	47.1	55.4	62.0	67.6	72.7	77.1
3.5	32.9	43.3	51.0	57.1	62.4	66.9	71.1
			L_∞ = 194.8 cm				
1.0	62.9	81.2	94.3	104.8	113.8	121.8	128.8
1.5	54.9	71.3	83.2	92.7	100.9	107.9	114.4
2.0	48.7	63.5	74.4	83.2	90.6	97.0	102.8
2.5	43.8	57.5	67.2	75.4	82.2	88.2	93.5
3.0	39.9	52.4	61.6	69.0	75.2	80.8	85.7
3.5	36.6	48.1	56.7	63.5	69.4	74.4	79.1
			L_∞ = 223.0 cm				
1.0	72.0	93.0	107.9	120.0	130.2	139.4	147.4
1.5	62.9	81.6	95.2	106.2	115.5	123.5	130.9
2.0	55.8	72.7	85.2	95.2	103.7	111.0	117.7
2.5	50.2	65.8	76.9	86.3	94.1	101.0	107.0
3.0	45.7	60.0	70.5	78.9	86.1	92.6	98.1
3.5	41.9	55.1	64.9	72.7	79.4	85.2	90.5

[1] Dashed lines encompass our reasonable range of values; underlined value is our most reasonable estimate.

reasonable range of estimates (deleting the unreasonably low $E = 0.12$), and the underlined value in the center of Table 1 is our most reasonable estimate. One can see in Table 1 that the values are all greater than the approximate absolute minimum size of 32.5 cm[11] for the Atlantic yellowfin tuna fishery over the range of the estimates of L_∞.

For the moment let us assume that recruitment is knife-edged at 32.5 cm (0.67 kg) and that the fishery can be regulated such to obtain a knife-edged recruitment at any desired size. Therefore, the maximum possible increases in yield per recruit may be computed. Our smallest reasonable values for optimal size at recruitment are 47.1 cm (2.0 kg), 52.4 cm (2.8 kg), or 60.0 cm (4.1 kg) depending on L_∞. The respective predicted values of yield per recruit are 2.0%, 3.1%, and 4.3% higher than when size at recruitment is 32.5 cm. Our largest reasonable estimates of optimal size at recruitment are 97.1 cm (17 kg), 107.9 cm (24 kg), or 123.5 cm (36 kg). The respective predicted increases in yield per recruit are 65%, 73%, and 82%. The predicted increase in yield per recruit using all of our most reasonable parameter estimates, i.e., raising 32.5 cm to 83.2 cm (11 kg), is 23%. The bounds on an increase in yield per recruit, 2% to 82%, and the most likely value of 23%, are estimated under the assumptions of knife-edged recruitment, and that size at recruitment represents an absolute minimum size. The Atlantic yellowfin tuna fishery, however, does not have knife-edged recruitment.

We used equation 1b of this paper to obtain our most reasonable estimate of the 1967-71 average effective minimum size for the Atlantic yellowfin tuna fishery from average lengths given in Table 15 of Lenarz and Sakagawa (1972, see footnote 5). The estimate of average effective minimum size is about 55 cm (3.2 kg). Nearly all the values within the dashed lines in Table 1, however, are greater than 55. The only smallest reasonable estimate of optimal effective minimum size greater than 55 cm is 60.0 cm with L_∞ = 223.0 cm. An increase from 55 to 60.0 cm would give an increase in yield per recruit $< 0.2\%$. The largest reasonable estimates of optimal effective minimum size predict increases in yield per recruit of 28%, 36%, or 45% with in-

[11] The value of 32.5 cm represents our selection for an approximate absolute minimum size for the Atlantic yellowfin tuna fishery, which also agrees with that chosen by Joseph and Tomlinson (1972, see footnote 4).

creases from 55 cm to 97.1, 107.9, and 123.5 cm, respectively depending on L_∞. The increase in yield per recruit by increasing the effective minimum size from 55 to 83.2 cm, our most reasonable estimate, is only 7.9%.

From the above analysis using a wide range of parameter estimates, we can conclude with reasonable assurance that virtually any increase in the effective minimum size will cause an increase in yield per recruit. Our most likely estimate of this increase in yield per recruit is only 7.9% which is bounded, with reasonable parameter estimates, by 0% and 45%.

Ricker Model

Ricker model yield-per-recruit isopleths were calculated using values of M of 0.6, 0.8, and 1.0 to illustrate our estimates of actual (rather than relative) yield per recruit (Figures 1, 2, and 3). As will be mentioned in the next section it is difficult to estimate the location of the fishery on the graphs, i.e., when fishing mortality is size specific it is not a trivial matter to make reasonable estimates of age at recruitment, t_r', and a constant total mortality coefficient, Z. Our most reasonable estimates, taken from Lenarz and Sakagawa (1972, see footnote 5), of these parameters are: t_r' is 1.41 yr and Z is 1.4.

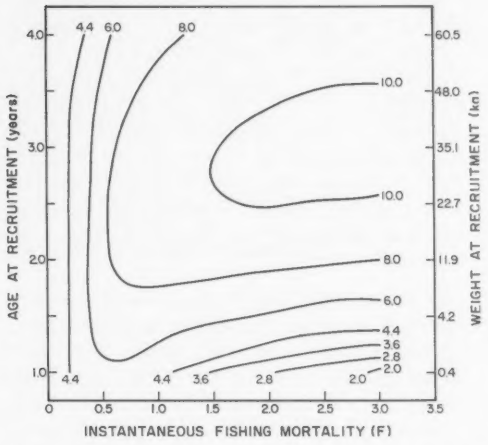

FIGURE 1.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 0.6$.

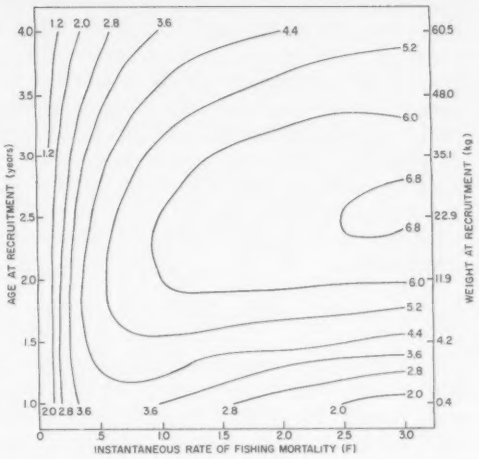

FIGURE 2.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 0.8$.

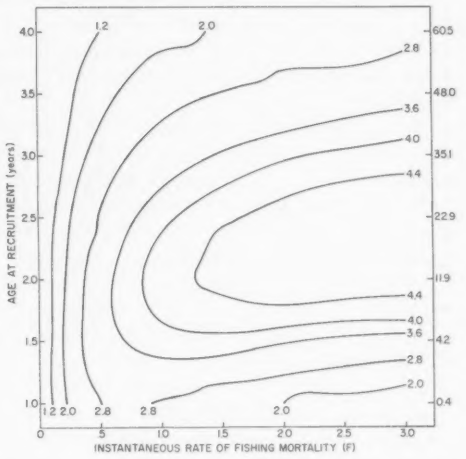

FIGURE 3.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 1.0$.

The results (Figures 1, 2, and 3) show, for example, that with $M = 0.6$ and Z remaining constant (1.4), an increase in age at recruitment from 1.41 to 1.83 yr (or 77.5 cm) raises the yield per recruit about 20%; if $M = 0.8$, the same change raises the yield per recruit on the order of 10%; and if $M = 1.0$, the same change does

not change yield per recruit. If age at recruitment is held constant and fishing mortality is doubled, when $M = 0.6$ yield per recruit decreases by some 20%; when $M = 0.8$ yield per recruit increases on the order of 5%; and when $M = 1.0$ yield per recruit increases about 30%. If effort is doubled and age at recruitment is raised to 1.83 yr, when $M = 0.6$ or $M = 0.8$ yield per recruit increases on the order of 20%; and when $M = 1.0$ yield per recruit increases by about 40%.

Estimation of t_r'

In employing a knife-edged approximation to size-specific recruitment protracted over some time period, the first problem is to determine the proper age at recruitment (t_r') such that the integration reflects the same yield per recruit as the size-specific recruitment case. There are two problems in doing so. First, there are two values for t_r' that will give the same yield per recruit as the size-specific recruitment case, unless eumetric fishing obtains. Often, however, this may be of little consequence, since one of the two values for t_r' could be obviously infeasible. Second, t_r' will depend on the fishing mortality.

Two estimators of t_r' are provided, at least implicitly, by Beverton and Holt (1957): (1) the age corresponding to the mean selection length, and (2) the resultant of a formula depending on Z and the average age, $\overline{t}$ (or average length, $\overline{l}$), in the catch. The mean selection length is the 50% selection length if the selection curve is symmetrical, and it is not dependent on the magnitude of the fishing mortality coefficient, F. The second estimator of t_r' is

$$t_r' = \overline{t} - 1/Z \tag{1a}$$

or, in terms of length

$$l_r' = \overline{l} - K(L_\infty - \overline{l})/Z. \tag{1b}$$

These two equations were obtained from manipulations of the Beverton and Holt yield equation.

Several computations of yield per recruit with the program GXPOPS were made utilizing $F = 0.1$ and $F = 2.0$, $M = 0.8$, the von Bertalanffy equation for Atlantic yellowfin tuna, and an arbitrary age-specific selection curve (Figure 4) in order to demonstrate the two problems and to evaluate the two estimators of t_r'. At $F = 0.1$, the values of t_r' giving the same yields per recruit as the selection curve are <8 mo (t_0 of the von Bertalanffy growth curve is 7.48 mo) or 24 mo, and 19 or 45 mo for $F = 2.0$. Since the state of the simulated fishery is not eumetric for either value of F, there are two knife-edged approximation locations. The effect of the magnitude of F on the true t_r' is obvious, with the lower value increasing from <8 to 19 mo and the upper value increasing from 24 to 45 mo as F is changed from 0.1 to 2.0. The reasonable values for t_r' to approximate the selection curve, however, are 24 mo for $F = 0.1$ and 19 mo for $F = 2.0$, a change of 5 mo.

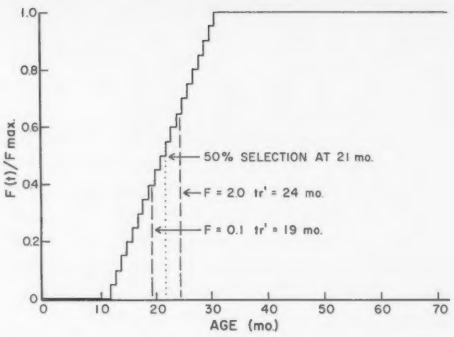

FIGURE 4.—Arbitrary age-specific recruitment curve.

Estimator 1, the mean selection age, is 21 mo and is shown along with the reasonable values in Figure 4. Using 21 mo for t_r' would result in yields per recruit that are 4% and 15% too high for $F = 0.1$ and $F = 2.0$ respectively. Estimator 1 does not change with F, of course, but in this case it lies intermediate between the true t_r' values. Estimator 2 gives 19 mo for $F = 0.1$ and 18 mo for $F = 2.0$. We emphasize that this estimator does depend on the magnitude of F.

Neither estimator is exact in this example where the catches, their ages, and the selection curve are known without error. This places doubt on their estimates from the usual catch at age data where considerable random error would be involved. Encouraging, though, is that both estimators indicate the proper direction that the fishery's selectivity should proceed to approach the optimal yield per recruit—about

15 mo for $F = 0.1$ and 30 mo for $F = 2.0$. Since estimator 1 requires size-selective data not frequently available and does not respond to changes in F, estimator 2 appears to be the most attractive for knife-edged approximations. The Atlantic yellowfin tuna fishery, however, has a much more complex recruitment pattern and size-specific F than this simple example owing to the diverse gear types. The mix of relative F among the various gear types makes the determination of the appropriate current t_r' somewhat tenuous.

Estimation of Constant Z

The yield-per-recruit isopleths shown in Figures 1, 2, and 3 were calculated under the assumption that fishing mortality and Z are constant after the fish are recruited. The value of Z was also estimated under the same assumption. The section on size-specific fishing mortality will indicate that F is not a constant, but is related to size. Thus our estimate of a constant Z may not be realistic but may be a more reasonable approach to estimating yield per recruit than the size-specific F approach given the quality of the data. It is the average of values of Z estimated for the FIS bait boat and purse seine fisheries (Lenarz and Sakagawa, 1972, see footnote 5). The size-specific F section indicates that F decreases with size for bait boats and increases with size for purse seiners. Beverton and Holt (1956) gave examples that indicated that when F decreases with age, constant Z will be overestimated and when F increases with age, constant Z will be underestimated. Hopefully we have obtained a reasonable estimate by taking the average of Z's for the two gears.

Size-Specific F Approach

Estimates of Length Frequencies

Length frequencies, numbers of yellowfin caught by 5-cm intervals starting at 35 cm (32.5 cm $\leq$ fork length $<$ 37.5 cm), were estimated for each gear and the total fishery for two overlapping periods, 1967-71 and 1969-71 (Figure 5). The first period was used with the hope that the effect caused by unequal strength of year classes would be minimized by averaging. The second period was used because it was felt that

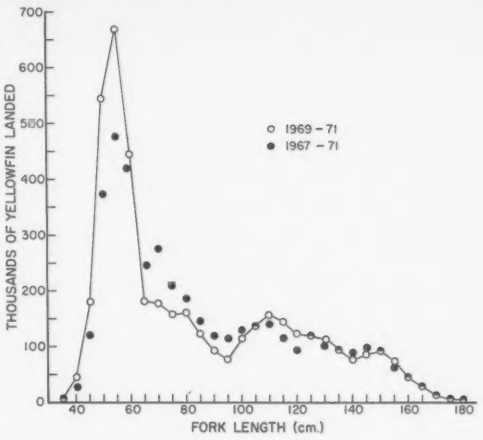

FIGURE 5.—Average length frequencies for the Atlantic yellowfin tuna fisheries for two periods, 1967-71 and 1969-71.

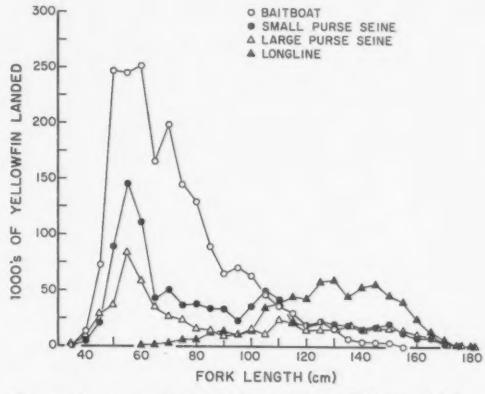

FIGURE 6.—Average length frequencies (1967-71) of Atlantic yellowfin tuna caught by four gear types.

the data are more accurate. Length frequencies of the two periods are quite similar and produce similar estimates of size-specific fishing mortality and estimates of yield per recruit. Thus, to avoid redundancy, only the data for the 1967-71 period are used. Figure 6 and Table 2 show the length frequencies for each gear. The curves are as described earlier (see introductory section.)

Estimates of Size-Specific Fishing Mortality

Size-specific instantaneous coefficients of fishing mortality were estimated with the method of Gulland (1965) and Murphy (1965) as suggested

TABLE 2.—Basic data on size (age) composition of catch of yellowfin tuna from the tropical Atlantic Ocean.

Midpoint of size interval (cm)	Weight at beginning of interval (kg)	Age at beginning of interval (yr)	1967-71 average number of yellowfin landed				
			Bait boats	Small purse seiners	Large purse seiners	Longliners	Total
35	0.67	1.0579	1,886	372	100		2,358
40	1.03	1.1325	14,551	5,445	9,057		29,053
45	1.49	1.2093	72,972	21,782	28,372		123,126
50	2.08	1.2888	246,924	89,614	36,684	7	373,229
55	2.79	1.3710	245,206	146,883	83,153	22	475,264
60	3.66	1.4562	251,017	110,755	59,648	451	421,871
65	4.69	1.5445	165,328	42,427	35,891	647	244,293
70	5.90	1.6363	197,855	49,929	26,992	2,151	276,927
75	7.30	1.7317	143,885	36,942	23,263	5,435	209,525
80	8.90	1.8310	128,810	37,082	15,528	5,694	187,114
85	10.72	1.9348	89,637	31,143	13,338	12,025	146,143
90	12.77	2.0432	64,128	31,135	9,818	13,049	118,130
95	15.06	2.1568	70,422	22,248	10,062	11,665	114,397
100	17.61	2.2761	63,619	36,483	13,323	15,074	128,499
105	20.43	2.4017	45,582	48,274	11,647	34,071	139,574
110	23.54	2.5343	36,414	42,283	24,296	40,209	143,202
115	26.95	2.6748	29,227	21,268	21,466	44,034	115,995
120	30.67	2.8240	18,877	18,311	15,144	42,859	95,191
125	34.72	2.9832	22,228	23,711	15,018	57,358	118,915
130	39.10	3.1538	15,152	20,612	16,238	58,544	110,546
135	43.84	3.3376	7,142	18,304	18,504	44,690	88,640
140	48.95	3.5368	4,137	15,790	13,569	52,070	85,566
145	54.43	3.7542	3,393	17,301	17,886	55,582	94,162
150	60.31	3.9935	3,459	20,222	16,711	45,648	86,040
155	66.60	4.2595	1,511	12,057	14,926	39,108	67,602
160	73.30	4.5590	793	8,754	10,678	24,489	44,714
165	80.44	4.9017	634	7,803	6,633	13,659	28,729
170	88.03	5.3021	327	2,470	2,918	6,265	11,980
175	96.07	5.7838	209	2,132	1,383	241	3,965
180	104.59	6.3883	49	1,429	361	55	1,894
	113.60	7.2004					
Total			1,945,374	942,961	573,207	625,102	4,086,645

by Lenarz (1971b).[12] We followed the modification of Joseph and Tomlinson (1972, see footnote 4) by using the inverse of the von Bertalanffy growth equation to convert size distributions to age distributions. This method assumes that there is a reasonably accurate relationship between length and age of yellowfin tuna. This assumption has not been verified. Ageing by modal progression would probably be more satisfactory, if more complete length composition data were available on a monthly or quarterly basis.

The reverse iterative procedure with computer program COHORT and $M = 0.8$ was used to estimate size-specific values of fishing mortality (F) starting at the 180-cm interval. Four initial values of F were tried: 0.2, 0.4, 0.6, and 0.8 (Figure 7). Estimates of F tend to converge as size of the yellowfin tuna decreases with the range of initial values tried as is characteristic

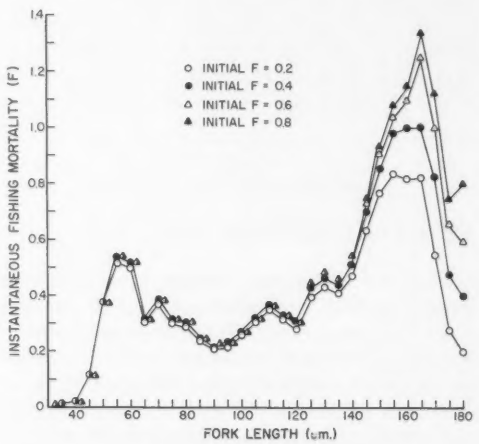

FIGURE 7.—Estimates of size-specific instantaneous fishing mortality coefficients (F) with several initial F values.

[12] Lenarz, W. 1971b. Yield per recruit of Atlantic yellowfin tuna for multigear fisheries. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

of the methodology (Tomlinson, 1970). Calculations of yield per recruit using initial values of F of 0.2 and 0.8 are shown in Figures 8 and 9 as functions of initial values of F, effort, and size at recruitment. The values of yield per recruit do not vary significantly (<10%) with changes in the initial values of F, and the relative values are quite similar. Values of size specific F are shown for each gear in Figure 10 when initial values of F are 0.2 and 0.8. When the initial value of F is 0.8, values of F for small purse seiners increase sharply with size from 170 to 180 cm. This does not occur when the initial value of F is 0.2. Intuitively we do not expect an increase in F with size past 170 cm and thus choose to use the results when the initial value of F is 0.2 in the remainder of the

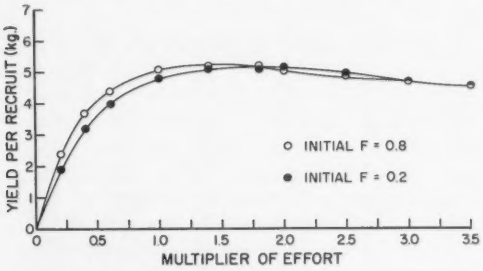

FIGURE 8.—Yield-per-recruit (kg) of Atlantic yellowfin tuna, when size at recruitment is 32.5 cm, as a function of the multiplier of fishing effort.

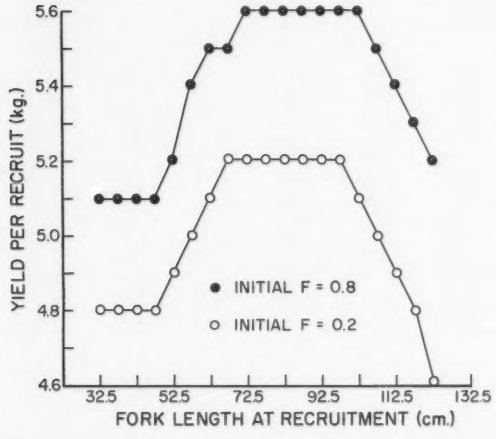

FIGURE 9.—Yield-per-recruit (kg) of Atlantic yellowfin tuna, with the current level of fishing effort, as a function of length at recruitment.

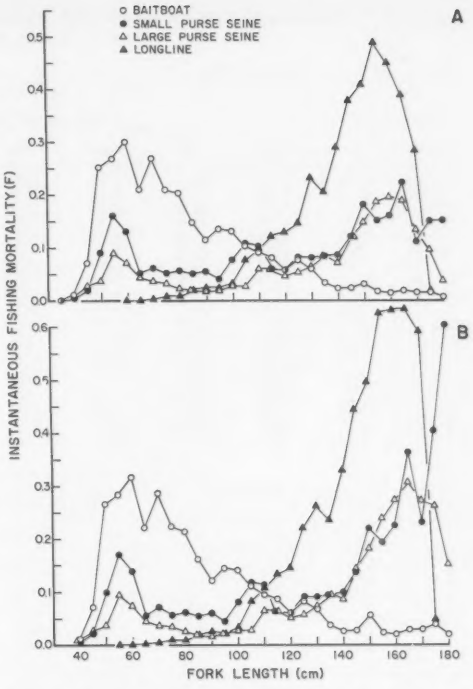

FIGURE 10.—Estimates of size-specific instantaneous fishing mortality coefficients (F) by gear type when initial values of F are (A) $F = 0.2$, (B) $F = 0.8$.

paper. Validity of the estimates of F depends on the validity of the assumption that recruitment has been fairly constant for the cohorts included in the analysis. The special ICCAT working group noted that the cohort which entered the surface fisheries in 1969 appears to be weaker than the following two cohorts (ICCAT, 1972, see footnote 2). Although inclusion of 5 yr of data in the analysis may minimize the source of error, future studies should examine the sensitivity of the results to errors of this type.

Estimates of Yield Per Recruit

Results of the yield-per-recruit calculations using the estimates of size-specific F when the initial value of F is 0.2 and with $M = 0.8$ are shown by gear in Table 3. Yield-per-recruit isopleths and the line of eumetric fishing (size at recruitment, $l^{*\prime}_r$, which maximizes yield per recruit at a given effort) for the entire fishery

TABLE 3.—Estimates of yield per recruit (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.08	0.15	0.21	0.31	0.39	0.46	0.49	0.56	0.62	0.68
117.5	30.6	0.09	0.17	0.24	0.36	0.46	0.54	0.58	0.66	0.73	0.80
112.5	26.9	0.11	0.21	0.29	0.43	0.55	0.65	0.69	0.80	0.89	0.96
107.5	23.5	0.13	0.24	0.33	0.50	0.64	0.75	0.80	0.92	1.02	1.11
102.5	20.4	0.15	0.27	0.38	0.57	0.73	0.86	0.92	1.06	1.17	1.27
97.5	17.6	0.17	0.31	0.44	0.66	0.85	1.01	1.08	1.24	1.38	1.50
92.5	15.0	0.19	0.35	0.50	0.75	0.96	1.15	1.23	1.41	1.58	1.72
87.5	12.7	0.20	0.38	0.54	0.81	1.04	1.24	1.32	1.52	1.69	1.84
82.5	10.7	0.22	0.41	0.58	0.88	1.12	1.34	1.43	1.64	1.82	1.98
77.5	8.9	0.24	0.45	0.63	0.95	1.22	1.45	1.55	1.78	1.97	2.13
72.5	7.3	0.26	0.48	0.68	1.02	1.30	1.54	1.64	1.87	2.07	2.23
67.5	5.9	0.27	0.51	0.72	1.08	1.38	1.62	1.73	1.96	2.14	2.30
62.5	4.7	0.29	0.53	0.75	1.12	1.41	1.65	1.76	1.98	2.16	2.30
57.5	3.7	0.30	0.56	0.78	1.15	1.43	1.66	1.76	1.96	2.11	2.22
52.5	2.8	0.31	0.57	0.79	1.15	1.42	1.63	1.72	1.88	2.00	2.08
47.5	2.1	0.31	0.58	0.80	1.15	1.42	1.61	1.69	1.84	1.94	2.00
42.5	1.5	0.31	0.58	0.80	1.15	1.41	1.60	1.68	1.82	1.91	1.97
37.5	1.0	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.96
32.5	0.7	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.34	0.58	0.75	0.97	1.09	1.16	1.19	1.24	1.28	1.31
117.5	30.6	0.35	0.60	0.77	0.99	1.11	1.18	1.21	1.27	1.30	1.33
112.5	26.9	0.36	0.61	0.79	1.01	1.13	1.20	1.23	1.28	1.31	1.34
107.5	23.5	0.38	0.64	0.83	1.06	1.20	1.28	1.32	1.38	1.43	1.47
102.5	20.4	0.40	0.67	0.87	1.12	1.27	1.37	1.41	1.49	1.55	1.60
97.5	17.6	0.41	0.69	0.89	1.14	1.30	1.40	1.44	1.52	1.59	1.64
92.5	15.0	0.41	0.70	0.90	1.15	1.30	1.39	1.43	1.50	1.56	1.61
87.5	12.7	0.42	0.71	0.91	1.16	1.31	1.40	1.44	1.51	1.56	1.60
82.5	10.7	0.42	0.71	0.91	1.16	1.30	1.39	1.43	1.49	1.53	1.57
77.5	8.9	0.43	0.71	0.91	1.15	1.29	1.37	1.40	1.45	1.49	1.51
72.5	7.3	0.43	0.71	0.91	1.14	1.27	1.34	1.36	1.41	1.43	1.44
67.5	5.9	0.43	0.72	0.91	1.13	1.24	1.30	1.32	1.35	1.36	1.35
62.5	4.7	0.43	0.71	0.90	1.11	1.22	1.27	1.28	1.30	1.29	1.28
57.5	3.7	0.43	0.71	0.90	1.10	1.19	1.23	1.24	1.24	1.23	1.21
52.5	2.8	0.44	0.72	0.89	1.08	1.16	1.19	1.20	1.19	1.17	1.14
47.5	2.1	0.44	0.71	0.89	1.06	1.13	1.15	1.15	1.14	1.11	1.07
42.5	1.5	0.44	0.71	0.88	1.06	1.12	1.14	1.14	1.11	1.08	1.05
37.5	1.0	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04
32.5	0.7	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.31	0.54	0.69	0.89	0.99	1.05	1.07	1.10	1.12	1.12
117.5	30.6	0.32	0.55	0.71	0.90	1.01	1.06	1.08	1.11	1.12	1.13
112.5	26.9	0.33	0.56	0.73	0.92	1.03	1.09	1.11	1.14	1.16	1.17
107.5	23.5	0.34	0.58	0.74	0.94	1.04	1.10	1.12	1.15	1.17	1.18
102.5	20.4	0.34	0.58	0.74	0.93	1.02	1.06	1.08	1.10	1.10	1.10
97.5	17.6	0.35	0.58	0.74	0.92	1.00	1.04	1.05	1.06	1.06	1.06
92.5	15.0	0.35	0.58	0.73	0.91	0.99	1.02	1.03	1.03	1.03	1.02
87.5	12.7	0.35	0.58	0.73	0.90	0.97	1.00	1.00	1.00	0.99	0.97
82.5	10.7	0.35	0.58	0.73	0.89	0.96	0.98	0.98	0.97	0.95	0.93
77.5	8.9	0.35	0.58	0.72	0.88	0.93	0.95	0.95	0.93	0.91	0.88
72.5	7.3	0.35	0.57	0.72	0.86	0.92	0.92	0.92	0.90	0.87	0.84
67.5	5.9	0.35	0.57	0.71	0.85	0.89	0.89	0.88	0.86	0.82	0.79
62.5	4.7	0.35	0.57	0.71	0.84	0.87	0.87	0.86	0.83	0.80	0.76
57.5	3.7	0.35	0.57	0.70	0.82	0.85	0.84	0.82	0.79	0.75	0.71
52.5	2.8	0.35	0.57	0.69	0.80	0.82	0.80	0.79	0.75	0.71	0.67
47.5	2.1	0.35	0.56	0.68	0.78	0.79	0.77	0.75	0.71	0.66	0.62
42.5	1.5	0.35	0.56	0.68	0.78	0.79	0.76	0.75	0.70	0.65	0.61
37.5	1.0	0.35	0.56	0.68	0.78	0.79	0.76	0.75	0.70	0.65	0.61
32.5	0.7	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61

TABLE 3.—Estimates of yield per recruit (kg) when M = 0.8, initial F = 0.2, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

		LONG LINERS									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.80	1.40	1.86	2.49	2.87	3.12	3.21	3.38	3.49	3.57
117.5	30.6	0.82	1.44	1.90	2.53	2.90	3.14	3.23	3.38	3.47	3.54
112.5	26.9	0.84	1.46	1.93	2.54	2.90	3.12	3.19	3.32	3.39	3.43
107.5	23.5	0.85	1.48	1.93	2.52	2.84	3.02	3.08	3.17	3.20	3.21
102.5	20.4	0.86	1.48	1.93	2.49	2.78	2.93	2.97	3.03	3.03	3.01
97.5	17.6	0.86	1.47	1.90	2.43	2.69	2.81	2.83	2.85	2.82	2.76
92.5	15.0	0.86	1.46	1.89	2.38	2.62	2.71	2.72	2.71	2.66	2.58
87.5	12.7	0.86	1.46	1.87	2.34	2.55	2.62	2.63	2.59	2.52	2.43
82.5	10.7	0.86	1.45	1.85	2.29	2.48	2.52	2.52	2.46	2.36	2.25
77.5	8.9	0.85	1.43	1.82	2.23	2.38	2.40	2.38	2.29	2.17	2.04
72.5	7.3	0.85	1.41	1.79	2.17	2.29	2.28	2.24	2.13	1.99	1.85
67.5	5.9	0.84	1.39	1.75	2.09	2.18	2.13	2.09	1.95	1.79	1.63
62.5	4.7	0.84	1.38	1.72	2.03	2.09	2.03	1.98	1.82	1.64	1.48
57.5	3.7	0.83	1.35	1.67	1.95	1.97	1.88	1.81	1.63	1.44	1.27
52.5	2.8	0.82	1.33	1.63	1.86	1.85	1.73	1.66	1.46	1.26	1.09
47.5	2.1	0.82	1.31	1.60	1.81	1.77	1.64	1.56	1.35	1.15	0.98
42.5	1.5	0.82	1.31	1.59	1.79	1.75	1.61	1.53	1.32	1.12	0.94
37.5	1.0	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
32.5	0.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94

are shown in Figure 11. Table 3 and Figures 8, 9, and 11 indicate that if size at recruitment remains constant at 32.5 cm, very little increase in yield per recruit (~5%) can be expected if effort is increased, and if effort remains constant, very little (~10%) increase in yield per recruit can be expected by increasing size at recruitment. However, if fishing effort is doubled (i.e., multiplier = 2.0) and size at recruitment increased to 55 cm (3.2 kg), yield per recruit would increase 15%, or if size at recruitment is increased to 77.5 cm (~10 kg), yield per recruit would increase about 30% (Table 3). Since the line of eumetric fishing shows that optimum size at recruitment changes with fishing effort, any "minimum size" regulation must be geared to fishing effort.

If fishermen are unable to distinguish the size of yellowfin before capturing them and a minimum size regulation prevents their landing, then the discarding of dead yellowfin will occur. Table 4 presents landings per recruit by gear and Figure 12 the landings per recruit for the total fishery when killing and discarding ("dumping") of all yellowfin smaller than the size limit occurs. If the minimum size limit is 55 cm and effort remains the same, then a 2.7% decrease in landings per recruit would occur; and a 13% decrease in landings per recruit would occur if the minimum size is set at 77.5 cm. If effort is doubled and the minimum size is 55 cm, then a 1% increase in landings per recruit would occur; with a minimum size of 77.5 cm, a 16% decline in landings per recruit would

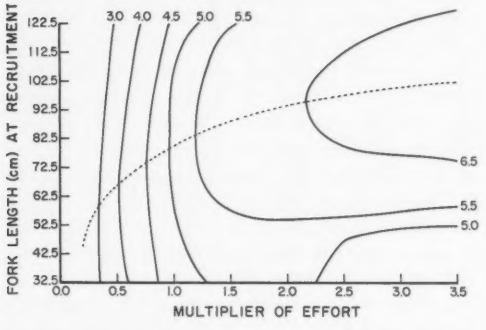

FIGURE 11.—Yield-per-recruit (kg) isopleths for the entire Atlantic yellowfin tuna fishery. Dotted curve is the line of eumetric fishing.

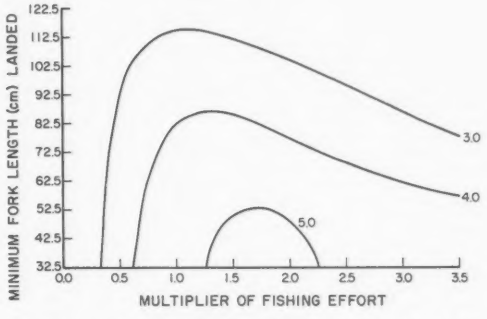

FIGURE 12.—Landings-per-recruit (kg) isopleths for Atlantic yellowfin tuna when all fish less than the minimum size that are caught are discarded dead.

TABLE 4.—Landings per recruit (kg) when $M = 0.8$, initial $F = 0.2$, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.07	0.12	0.15	0.18	0.18	0.17	0.16	0.14	0.12	0.10
117.5	30.6	0.08	0.14	0.18	0.22	0.22	0.22	0.21	0.19	0.16	0.14
112.5	26.9	0.10	0.17	0.22	0.27	0.29	0.28	0.28	0.25	0.22	0.19
107.5	23.5	0.12	0.20	0.26	0.33	0.36	0.36	0.36	0.33	0.30	0.27
102.5	20.4	0.14	0.24	0.31	0.40	0.44	0.45	0.44	0.42	0.39	0.35
97.5	17.6	0.16	0.27	0.36	0.48	0.53	0.56	0.56	0.54	0.51	0.47
92.5	15.0	0.18	0.31	0.41	0.55	0.63	0.66	0.67	0.66	0.63	0.59
87.5	12.7	0.19	0.34	0.45	0.61	0.70	0.74	0.75	0.75	0.73	0.69
82.5	10.7	0.21	0.37	0.50	0.68	0.79	0.84	0.86	0.87	0.85	0.81
77.5	8.9	0.23	0.41	0.55	0.76	0.89	0.97	0.99	1.01	1.00	0.97
72.5	7.3	0.25	0.44	0.60	0.84	0.99	1.08	1.11	1.15	1.15	1.12
67.5	5.9	0.27	0.48	0.66	0.92	1.10	1.22	1.25	1.31	1.33	1.32
62.5	4.7	0.28	0.51	0.70	0.98	1.18	1.31	1.35	1.43	1.46	1.46
57.5	3.7	0.29	0.54	0.74	1.05	1.27	1.42	1.48	1.57	1.62	1.64
52.5	2.8	0.30	0.56	0.77	1.10	1.34	1.51	1.57	1.69	1.76	1.79
47.5	2.1	0.31	0.57	0.79	1.14	1.39	1.58	1.65	1.79	1.87	1.92
42.5	1.5	0.31	0.58	0.80	1.15	1.41	1.59	1.67	1.81	1.90	1.95
37.5	1.0	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95
32.5	0.7	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.31	0.47	0.54	0.56	0.50	0.43	0.40	0.31	0.25	0.19
117.5	30.6	0.32	0.49	0.57	0.60	0.55	0.48	0.44	0.36	0.29	0.23
112.5	26.9	0.33	0.51	0.60	0.64	0.59	0.53	0.49	0.41	0.33	0.27
107.5	23.5	0.35	0.55	0.65	0.71	0.68	0.62	0.58	0.50	0.42	0.35
102.5	20.4	0.37	0.58	0.70	0.78	0.76	0.71	0.68	0.60	0.52	0.45
97.5	17.6	0.38	0.61	0.73	0.82	0.81	0.77	0.74	0.66	0.59	0.51
92.5	15.0	0.39	0.62	0.75	0.84	0.84	0.80	0.78	0.70	0.62	0.55
87.5	12.7	0.40	0.63	0.76	0.87	0.88	0.84	0.82	0.75	0.67	0.60
82.5	10.7	0.40	0.64	0.78	0.90	0.91	0.88	0.85	0.79	0.71	0.64
77.5	8.9	0.41	0.65	0.80	0.92	0.94	0.91	0.89	0.83	0.76	0.69
72.5	7.3	0.41	0.66	0.81	0.94	0.96	0.94	0.92	0.86	0.79	0.73
67.5	5.9	0.42	0.67	0.82	0.96	0.99	0.98	0.96	0.90	0.84	0.77
62.5	4.7	0.42	0.68	0.83	0.98	1.01	1.00	0.98	0.93	0.87	0.81
57.5	3.7	0.43	0.69	0.85	1.01	1.05	1.05	1.04	1.00	0.95	0.89
52.5	2.8	0.43	0.70	0.87	1.04	1.10	1.10	1.10	1.07	1.03	0.98
47.5	2.1	0.44	0.71	0.88	1.05	1.11	1.13	1.13	1.10	1.07	1.03
42.5	1.5	0.44	0.71	0.88	1.05	1.12	1.13	1.13	1.11	1.08	1.04
37.5	1.0	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04
32.5	0.7	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.28	0.43	0.50	0.51	0.46	0.39	0.36	0.28	0.21	0.16
117.5	30.6	0.29	0.45	0.52	0.54	0.50	0.43	0.39	0.31	0.25	0.19
112.5	26.9	0.30	0.47	0.55	0.59	0.54	0.48	0.44	0.36	0.29	0.24
107.5	23.5	0.31	0.49	0.58	0.63	0.59	0.53	0.50	0.42	0.35	0.28
102.5	20.4	0.32	0.50	0.59	0.64	0.61	0.55	0.52	0.44	0.37	0.31
97.5	17.6	0.32	0.51	0.60	0.66	0.63	0.57	0.54	0.46	0.39	0.33
92.5	15.0	0.33	0.51	0.61	0.67	0.64	0.59	0.56	0.48	0.41	0.35
87.5	12.7	0.33	0.52	0.62	0.68	0.65	0.60	0.57	0.50	0.42	0.36
82.5	10.7	0.33	0.52	0.62	0.69	0.67	0.62	0.59	0.51	0.44	0.38
77.5	8.9	0.33	0.53	0.63	0.70	0.68	0.63	0.60	0.53	0.46	0.40
72.5	7.3	0.34	0.53	0.64	0.71	0.70	0.65	0.62	0.55	0.49	0.43
67.5	5.9	0.34	0.54	0.65	0.72	0.71	0.67	0.64	0.57	0.51	0.45
62.5	4.7	0.34	0.54	0.65	0.74	0.73	0.69	0.66	0.60	0.54	0.48
57.5	3.7	0.35	0.55	0.66	0.75	0.75	0.71	0.69	0.63	0.58	0.53
52.5	2.8	0.35	0.56	0.68	0.77	0.77	0.74	0.73	0.67	0.62	0.58
47.5	2.1	0.35	0.56	0.68	0.77	0.78	0.75	0.74	0.69	0.64	0.60
42.5	1.5	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
37.5	1.0	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
32.5	0.7	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61

TABLE 4.—Landings per recruit (kg) when $M = 0.8$, initial $F = 0.2$, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.—Continued.

		LONG LINERS									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.72	1.13	1.34	1.43	1.33	1.16	1.07	0.85	0.67	0.52
117.5	30.6	0.74	1.18	1.41	1.53	1.43	1.27	1.18	0.96	0.76	0.60
112.5	26.9	0.77	1.22	1.47	1.61	1.53	1.37	1.28	1.06	0.86	0.69
107.5	23.5	0.79	1.25	1.51	1.68	1.61	1.45	1.37	1.15	0.94	0.77
102.5	20.4	0.80	1.28	1.55	1.72	1.67	1.52	1.43	1.21	1.01	0.84
97.5	17.6	0.81	1.29	1.56	1.74	1.69	1.54	1.46	1.24	1.04	0.86
92.5	15.0	0.81	1.29	1.57	1.76	1.70	1.56	1.48	1.26	1.06	0.88
87.5	12.7	0.81	1.30	1.58	1.77	1.72	1.58	1.49	1.28	1.08	0.90
82.5	10.7	0.81	1.30	1.58	1.78	1.73	1.59	1.51	1.30	1.10	0.92
77.5	8.9	0.82	1.31	1.59	1.78	1.74	1.60	1.51	1.30	1.10	0.93
72.5	7.3	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.93
67.5	5.9	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
62.5	4.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
57.5	3.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
52.5	2.8	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
47.5	2.1	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
42.5	1.5	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
37.5	1.0	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
32.5	0.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94

occur. Therefore, if effort is constant the predicted gain with no dumping is greater than the possible loss through dumping if the minimum size were 55 cm, but at 77.5 cm the opposite is true. At both size limits we predict a greater gain with no dumping than possible loss through dumping if effort is doubled.

Assuming constant recruitment, yield per recruit per unit effort is a measure of fishing success. Table 5 presents the estimated yield per recruit per effort by gear assuming no dumping. Increasing the size at recruitment to 77.5 cm at the current level of effort would result in a 17% decrease for bait boats, a 9% increase for small purse seiners, a 12% increase for large purse seiners, and a 25% increase for longliners. Yield per recruit per effort would drop by about 35% for each of the gears if effort doubled and size at recruitment increased to 77.5 cm. If effort doubled and size at recruitment remained 32.5 cm, yield per recruit per effort would decrease by 30% for bait boats, 50% for purse seiners, and 60% for longliners.

Changes in the average weight of landings should be considered because average weight affects the values of landings particularly in light of size-specific changes in the value of yellowfin tuna. Table 6 presents estimates of the average weight of catches by gear. Figure 13 shows average weight isopleths for the entire fishery. If effort remained constant and size at recruitment increased to 77.5 cm, the average weight of the catch of the total fishery would increase from 17.7 kg to 30.3 kg. If effort doubled and size at recruitment increased to 77.5 cm, the average weight would increase to 24.2 kg.

Sensitivity of Results to Errors when Ageing Large Yellowfin

The growth curve used in this study was based on the use of modal progressions to age yellowfin. Unfortunately while this method is probably reasonably accurate for ageing yellowfin less than about 130 cm long, beyond this size it becomes increasingly difficult to separate modes, and there is a reasonable probability that ages are increasingly underestimated with increases in size. In addition, because tuna apparently spawn over a large portion of the year, the exact meaning of age is not always clear. Alternative methods, such as ageing by

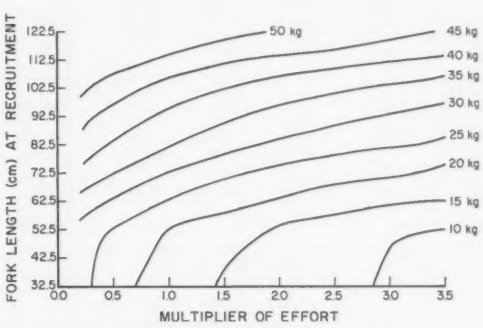

FIGURE 13.—Average weight (kg) isopleths for the entire Atlantic yellowfin tuna fishery.

TABLE 4.—Landings per recruit (kg) when $M = 0.8$, initial $F = 0.2$, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.07	0.12	0.15	0.18	0.18	0.17	0.16	0.14	0.12	0.10
117.5	30.6	0.08	0.14	0.18	0.22	0.22	0.22	0.21	0.19	0.16	0.14
112.5	26.9	0.10	0.17	0.22	0.27	0.29	0.28	0.28	0.25	0.22	0.19
107.5	23.5	0.12	0.20	0.26	0.33	0.36	0.36	0.36	0.33	0.30	0.27
102.5	20.4	0.14	0.24	0.31	0.40	0.44	0.45	0.44	0.42	0.39	0.35
97.5	17.6	0.16	0.27	0.36	0.48	0.53	0.56	0.56	0.54	0.51	0.47
92.5	15.0	0.18	0.31	0.41	0.55	0.63	0.66	0.67	0.66	0.63	0.59
87.5	12.7	0.19	0.34	0.45	0.61	0.70	0.74	0.75	0.75	0.73	0.69
82.5	10.7	0.21	0.37	0.50	0.68	0.79	0.84	0.86	0.87	0.85	0.81
77.5	8.9	0.23	0.41	0.55	0.76	0.89	0.97	0.99	1.01	1.00	0.97
72.5	7.3	0.25	0.44	0.60	0.84	0.99	1.08	1.11	1.15	1.15	1.12
67.5	5.9	0.27	0.48	0.66	0.92	1.10	1.22	1.25	1.31	1.33	1.32
62.5	4.7	0.28	0.51	0.70	0.98	1.18	1.31	1.35	1.43	1.46	1.46
57.5	3.7	0.29	0.54	0.74	1.05	1.27	1.42	1.48	1.57	1.62	1.64
52.5	2.8	0.30	0.56	0.77	1.10	1.34	1.51	1.57	1.69	1.76	1.79
47.5	2.1	0.31	0.57	0.79	1.14	1.39	1.58	1.65	1.79	1.87	1.92
42.5	1.5	0.31	0.58	0.80	1.15	1.41	1.59	1.67	1.81	1.90	1.95
37.5	1.0	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95
32.5	0.7	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.31	0.47	0.54	0.56	0.50	0.43	0.40	0.31	0.25	0.19
117.5	30.6	0.32	0.49	0.57	0.60	0.55	0.48	0.44	0.36	0.29	0.23
112.5	26.9	0.33	0.51	0.60	0.64	0.59	0.53	0.49	0.41	0.33	0.27
107.5	23.5	0.35	0.55	0.65	0.71	0.68	0.62	0.58	0.50	0.42	0.35
102.5	20.4	0.37	0.58	0.70	0.78	0.76	0.71	0.68	0.60	0.52	0.45
97.5	17.6	0.38	0.61	0.73	0.82	0.81	0.77	0.74	0.66	0.59	0.51
92.5	15.0	0.39	0.62	0.75	0.84	0.84	0.80	0.78	0.70	0.62	0.55
87.5	12.7	0.40	0.63	0.76	0.87	0.88	0.84	0.82	0.75	0.67	0.60
82.5	10.7	0.40	0.64	0.78	0.90	0.91	0.88	0.85	0.79	0.71	0.64
77.5	8.9	0.41	0.65	0.80	0.92	0.94	0.91	0.89	0.83	0.76	0.69
72.5	7.3	0.41	0.66	0.81	0.94	0.96	0.94	0.92	0.86	0.79	0.73
67.5	5.9	0.42	0.67	0.82	0.96	0.99	0.98	0.96	0.90	0.84	0.77
62.5	4.7	0.42	0.68	0.83	0.98	1.01	1.00	0.98	0.93	0.87	0.81
57.5	3.7	0.43	0.69	0.85	1.01	1.05	1.05	1.04	1.00	0.95	0.89
52.5	2.8	0.43	0.70	0.87	1.04	1.10	1.10	1.10	1.07	1.03	0.98
47.5	2.1	0.44	0.71	0.88	1.05	1.11	1.13	1.13	1.10	1.07	1.03
42.5	1.5	0.44	0.71	0.88	1.05	1.12	1.13	1.13	1.11	1.08	1.04
37.5	1.0	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04
32.5	0.7	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.28	0.43	0.50	0.51	0.46	0.39	0.36	0.28	0.21	0.16
117.5	30.6	0.29	0.45	0.52	0.54	0.50	0.43	0.39	0.31	0.25	0.19
112.5	26.9	0.30	0.47	0.55	0.59	0.54	0.48	0.44	0.36	0.29	0.24
107.5	23.5	0.31	0.49	0.58	0.63	0.59	0.53	0.50	0.42	0.35	0.28
102.5	20.4	0.32	0.50	0.59	0.64	0.61	0.55	0.52	0.44	0.37	0.31
97.5	17.6	0.32	0.51	0.60	0.66	0.63	0.57	0.54	0.46	0.39	0.33
92.5	15.0	0.33	0.51	0.61	0.67	0.64	0.59	0.56	0.48	0.41	0.35
87.5	12.7	0.33	0.52	0.62	0.68	0.65	0.60	0.57	0.50	0.42	0.36
82.5	10.7	0.33	0.52	0.62	0.69	0.67	0.62	0.59	0.51	0.44	0.38
77.5	8.9	0.33	0.53	0.63	0.70	0.68	0.63	0.60	0.53	0.46	0.40
72.5	7.3	0.34	0.53	0.64	0.71	0.70	0.65	0.62	0.55	0.49	0.43
67.5	5.9	0.34	0.54	0.65	0.72	0.71	0.67	0.64	0.57	0.51	0.45
62.5	4.7	0.34	0.54	0.65	0.74	0.73	0.69	0.66	0.60	0.54	0.48
57.5	3.7	0.35	0.55	0.66	0.75	0.75	0.71	0.69	0.63	0.58	0.53
52.5	2.8	0.35	0.56	0.68	0.77	0.77	0.74	0.73	0.67	0.62	0.58
47.5	2.1	0.35	0.56	0.68	0.77	0.78	0.75	0.74	0.69	0.64	0.60
42.5	1.5	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
37.5	1.0	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
32.5	0.7	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61

TABLE 4.—Landings per recruit (kg) when $M = 0.8$, initial $F = 0.2$, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.—Continued.

		LONG LINERS									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.72	1.13	1.34	1.43	1.33	1.16	1.07	0.85	0.67	0.52
117.5	30.6	0.74	1.18	1.41	1.53	1.43	1.27	1.18	0.96	0.76	0.60
112.5	26.9	0.77	1.22	1.47	1.61	1.53	1.37	1.28	1.06	0.86	0.69
107.5	23.5	0.79	1.25	1.51	1.68	1.61	1.45	1.37	1.15	0.94	0.77
102.5	20.4	0.80	1.28	1.55	1.72	1.67	1.52	1.43	1.21	1.01	0.84
97.5	17.6	0.81	1.29	1.56	1.74	1.69	1.54	1.46	1.24	1.04	0.86
92.5	15.0	0.81	1.29	1.57	1.76	1.70	1.56	1.48	1.26	1.06	0.88
87.5	12.7	0.81	1.30	1.58	1.77	1.72	1.58	1.49	1.28	1.08	0.90
82.5	10.7	0.81	1.30	1.58	1.78	1.73	1.59	1.51	1.30	1.10	0.92
77.5	8.9	0.82	1.31	1.59	1.78	1.74	1.60	1.51	1.30	1.10	0.93
72.5	7.3	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.93
67.5	5.9	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
62.5	4.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
57.5	3.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
52.5	2.8	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
47.5	2.1	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
42.5	1.5	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
37.5	1.0	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
32.5	0.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94

occur. Therefore, if effort is constant the predicted gain with no dumping is greater than the possible loss through dumping if the minimum size were 55 cm, but at 77.5 cm the opposite is true. At both size limits we predict a greater gain with no dumping than possible loss through dumping if effort is doubled.

Assuming constant recruitment, yield per recruit per unit effort is a measure of fishing success. Table 5 presents the estimated yield per recruit per effort by gear assuming no dumping. Increasing the size at recruitment to 77.5 cm at the current level of effort would result in a 17% decrease for bait boats, a 9% increase for small purse seiners, a 12% increase for large purse seiners, and a 25% increase for longliners. Yield per recruit per effort would drop by about 35% for each of the gears if effort doubled and size at recruitment increased to 77.5 cm. If effort doubled and size at recruitment remained 32.5 cm, yield per recruit per effort would decrease by 30% for bait boats, 50% for purse seiners, and 60% for longliners.

Changes in the average weight of landings should be considered because average weight affects the values of landings particularly in light of size-specific changes in the value of yellowfin tuna. Table 6 presents estimates of the average weight of catches by gear. Figure 13 shows average weight isopleths for the entire fishery. If effort remained constant and size at recruitment increased to 77.5 cm, the average weight of the catch of the total fishery would increase from 17.7 kg to 30.3 kg. If effort doubled and size at recruitment increased to 77.5 cm, the average weight would increase to 24.2 kg.

Sensitivity of Results to Errors when Ageing Large Yellowfin

The growth curve used in this study was based on the use of modal progressions to age yellowfin. Unfortunately while this method is probably reasonably accurate for ageing yellowfin less than about 130 cm long, beyond this size it becomes increasingly difficult to separate modes, and there is a reasonable probability that ages are increasingly underestimated with increases in size. In addition, because tuna apparently spawn over a large portion of the year, the exact meaning of age is not always clear. Alternative methods, such as ageing by

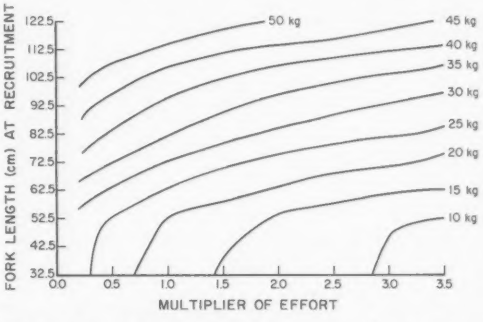

FIGURE 13.—Average weight (kg) isopleths for the entire Atlantic yellowfin tuna fishery.

TABLE 5.—Estimates of yield per recruit per effort (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.40	0.37	0.35	0.31	0.28	0.25	0.24	0.22	0.21	0.19
117.5	30.6	0.47	0.43	0.40	0.36	0.33	0.30	0.29	0.26	0.24	0.23
112.5	26.9	0.55	0.51	0.48	0.43	0.39	0.36	0.35	0.32	0.30	0.28
107.5	23.5	0.64	0.60	0.56	0.50	0.45	0.42	0.40	0.37	0.34	0.32
102.5	20.4	0.73	0.68	0.64	0.57	0.52	0.48	0.46	0.42	0.39	0.36
97.5	17.6	0.84	0.78	0.74	0.66	0.61	0.56	0.54	0.50	0.46	0.43
92.5	15.0	0.94	0.88	0.83	0.75	0.69	0.64	0.61	0.57	0.53	0.49
87.5	12.7	1.01	0.95	0.90	0.81	0.74	0.69	0.66	0.61	0.56	0.53
82.5	10.7	1.09	1.03	0.97	0.88	0.80	0.74	0.72	0.66	0.61	0.57
77.5	8.9	1.19	1.12	1.06	0.95	0.87	0.81	0.78	0.71	0.66	0.61
72.5	7.3	1.28	1.20	1.13	1.02	0.93	0.85	0.82	0.75	0.69	0.64
67.5	5.9	1.37	1.28	1.21	1.08	0.98	0.90	0.86	0.78	0.71	0.66
62.5	4.7	1.43	1.34	1.25	1.12	1.01	0.92	0.88	0.79	0.72	0.66
57.5	3.7	1.49	1.39	1.30	1.15	1.02	0.92	0.88	0.78	0.70	0.64
52.5	2.8	1.54	1.42	1.32	1.15	1.02	0.91	0.86	0.75	0.67	0.60
47.5	2.1	1.57	1.44	1.33	1.15	1.01	0.90	0.84	0.74	0.65	0.57
42.5	1.5	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.73	0.64	0.56
37.5	1.0	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.72	0.63	0.56
32.5	0.7	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.72	0.63	0.56

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	1.72	1.46	1.26	0.97	0.78	0.65	0.60	0.50	0.43	0.38
117.5	30.6	1.77	1.50	1.29	0.99	0.79	0.66	0.61	0.51	0.43	0.38
112.5	26.9	1.82	1.54	1.31	1.01	0.80	0.67	0.61	0.51	0.44	0.38
107.5	23.5	1.91	1.61	1.38	1.06	0.85	0.71	0.66	0.55	0.48	0.42
102.5	20.4	1.99	1.69	1.45	1.12	0.90	0.76	0.70	0.59	0.52	0.46
97.5	17.6	2.05	1.73	1.48	1.14	0.93	0.78	0.72	0.61	0.53	0.47
92.5	15.0	2.07	1.74	1.49	1.15	0.93	0.77	0.72	0.60	0.52	0.46
87.5	12.7	2.10	1.76	1.51	1.16	0.93	0.78	0.72	0.60	0.52	0.46
82.5	10.7	2.12	1.78	1.52	1.16	0.93	0.77	0.71	0.60	0.51	0.45
77.5	8.9	2.13	1.78	1.52	1.15	0.92	0.76	0.70	0.58	0.50	0.43
72.5	7.3	2.14	1.79	1.52	1.14	0.91	0.74	0.68	0.56	0.48	0.41
67.5	5.9	2.15	1.79	1.51	1.13	0.89	0.72	0.66	0.54	0.45	0.39
62.5	4.7	2.16	1.78	1.50	1.11	0.87	0.70	0.64	0.52	0.43	0.37
57.5	3.7	2.17	1.79	1.50	1.10	0.85	0.68	0.62	0.50	0.41	0.35
52.5	2.8	2.19	1.79	1.49	1.08	0.83	0.66	0.60	0.48	0.39	0.33
47.5	2.1	2.19	1.78	1.48	1.06	0.81	0.64	0.58	0.45	0.37	0.31
42.5	1.5	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.45	0.36	0.30
37.5	1.0	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.44	0.36	0.30
32.5	0.7	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.44	0.36	0.30

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	1.57	1.34	1.16	0.89	0.71	0.58	0.53	0.44	0.37	0.32
117.5	30.6	1.61	1.37	1.18	0.90	0.72	0.59	0.54	0.44	0.37	0.32
112.5	26.9	1.66	1.41	1.21	0.92	0.74	0.60	0.55	0.46	0.39	0.33
107.5	23.5	1.71	1.44	1.24	0.94	0.75	0.61	0.56	0.46	0.39	0.34
102.5	20.4	1.72	1.44	1.23	0.93	0.73	0.59	0.54	0.44	0.37	0.32
97.5	17.6	1.73	1.45	1.23	0.92	0.72	0.58	0.53	0.43	0.35	0.30
92.5	15.0	1.74	1.45	1.22	0.91	0.71	0.57	0.51	0.41	0.34	0.29
87.5	12.7	1.74	1.45	1.22	0.90	0.69	0.56	0.50	0.40	0.33	0.28
82.5	10.7	1.74	1.44	1.21	0.89	0.68	0.54	0.49	0.39	0.32	0.27
77.5	8.9	1.75	1.44	1.20	0.88	0.67	0.53	0.47	0.37	0.30	0.25
72.5	7.3	1.75	1.44	1.20	0.86	0.65	0.51	0.46	0.36	0.29	0.24
67.5	5.9	1.75	1.43	1.19	0.85	0.64	0.49	0.44	0.34	0.27	0.23
62.5	4.7	1.76	1.43	1.18	0.84	0.62	0.48	0.43	0.33	0.27	0.22
57.5	3.7	1.76	1.42	1.17	0.82	0.60	0.46	0.41	0.32	0.25	0.20
52.5	2.8	1.76	1.42	1.15	0.80	0.59	0.45	0.40	0.30	0.24	0.19
47.5	2.1	1.76	1.40	1.14	0.78	0.57	0.43	0.38	0.29	0.22	0.18
42.5	1.5	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.18
37.5	1.0	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.17
32.5	0.7	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.17

TABLE 5.—Estimates of yield per recruit per effort (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

LONG LINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	4.00	3.51	3.10	2.49	2.05	1.74	1.61	1.35	1.16	1.02
117.5	30.6	4.12	3.60	3.17	2.53	2.07	1.75	1.61	1.35	1.16	1.01
112.5	26.9	4.21	3.66	3.21	2.54	2.07	1.73	1.60	1.33	1.13	0.98
107.5	23.5	4.27	3.69	3.22	2.52	2.03	1.68	1.54	1.27	1.07	0.92
102.5	20.4	4.31	3.70	3.21	2.49	1.99	1.63	1.49	1.21	1.01	0.86
97.5	17.6	4.31	3.68	3.17	2.43	1.92	1.56	1.42	1.14	0.94	0.79
92.5	15.0	4.30	3.66	3.14	2.38	1.87	1.50	1.36	1.08	0.89	0.74
87.5	12.7	4.30	3.64	3.11	2.34	1.82	1.46	1.31	1.04	0.84	0.69
82.5	10.7	4.29	3.61	3.08	2.29	1.77	1.40	1.26	0.98	0.79	0.64
77.5	8.9	4.27	3.57	3.03	2.23	1.70	1.33	1.19	0.92	0.72	0.58
72.5	7.3	4.24	3.53	2.98	2.17	1.63	1.26	1.12	0.85	0.66	0.53
67.5	5.9	4.21	3.49	2.91	2.09	1.55	1.19	1.05	0.78	0.60	0.47
62.5	4.7	4.19	3.45	2.86	2.03	1.49	1.13	0.99	0.73	0.55	0.42
57.5	3.7	4.15	3.39	2.79	1.95	1.40	1.04	0.91	0.65	0.49	0.36
52.5	2.8	4.12	3.33	2.72	1.86	1.32	0.96	0.83	0.58	0.42	0.31
47.5	2.1	4.09	3.29	2.67	1.81	1.26	0.91	0.78	0.54	0.38	0.28
42.5	1.5	4.08	3.27	2.65	1.79	1.25	0.89	0.76	0.53	0.37	0.27
37.5	1.0	4.08	3.27	2.65	1.78	1.24	0.89	0.76	0.52	0.37	0.27
32.5	0.7	4.08	3.27	2.65	1.78	1.24	0.89	0.76	0.52	0.37	0.27

ENTIRE FISHERY

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	7.70	6.68	5.86	4.65	3.82	3.22	2.98	2.51	2.17	1.91
117.5	30.6	7.97	6.90	6.04	4.78	3.91	3.29	3.05	2.57	2.21	1.94
112.5	26.9	8.25	7.12	6.22	4.90	4.00	3.36	3.11	2.61	2.25	1.97
107.5	23.5	8.53	7.34	6.40	5.02	4.08	3.42	3.16	2.65	2.27	1.99
102.5	20.4	8.75	7.51	6.53	5.10	4.14	3.46	3.19	2.67	2.28	2.00
97.5	17.6	8.92	7.64	6.62	5.16	4.17	3.48	3.20	2.67	2.28	1.99
92.5	15.0	9.04	7.73	6.69	5.19	4.19	3.48	3.21	2.67	2.27	1.98
87.5	12.7	9.14	7.80	6.74	5.21	4.19	3.48	3.20	2.65	2.26	1.96
82.5	10.7	9.24	7.86	6.78	5.22	4.18	3.46	3.18	2.62	2.22	1.92
77.5	8.9	9.34	7.92	6.81	5.22	4.16	3.42	3.14	2.58	2.18	1.88
72.5	7.3	9.42	7.96	6.82	5.19	4.12	3.38	3.09	2.52	2.12	1.82
67.5	5.9	9.49	7.99	6.82	5.15	4.06	3.30	3.01	2.44	2.04	1.74
62.5	4.7	9.54	7.99	6.80	5.10	4.00	3.23	2.94	2.37	1.97	1.66
57.5	3.7	9.58	7.98	6.75	5.01	3.88	3.11	2.81	2.25	1.84	1.55
52.5	2.8	9.60	7.95	6.68	4.90	3.75	2.98	2.68	2.11	1.71	1.42
47.5	2.1	9.61	7.91	6.61	4.81	3.65	2.87	2.58	2.01	1.62	1.33
42.5	1.5	9.60	7.90	6.59	4.78	3.62	2.84	2.54	1.98	1.59	1.31
37.5	1.0	9.60	7.89	6.59	4.77	3.61	2.83	2.53	1.97	1.58	1.30
32.5	0.7	9.60	7.89	6.59	4.77	3.61	2.83	2.53	1.97	1.58	1.30

the examination of hard parts, are extremely difficult and not easily interpreted for tropical species such as the yellowfin tuna.

The marked increase in estimates of size-specific F beyond 130 cm for the purse seine gears is a possible result of underestimating ages of older yellowfin. To examine this possibility, the growth curve of LeGuen and Sakagawa (1973) was modified. It was hypothetically assumed that the percentage of underestimation of the time interval within a size interval increased linearly from 0% at 135 cm to 100% at 180 cm. The resulting growth curve is compared to the original in Figure 14.

Values of size-specific F were then estimated as before with initial values of 0.2 and 0.8. The value of 0.2 gave the most reasonable results for reasons similar to those given before. Values of size specific F for each gear are shown in

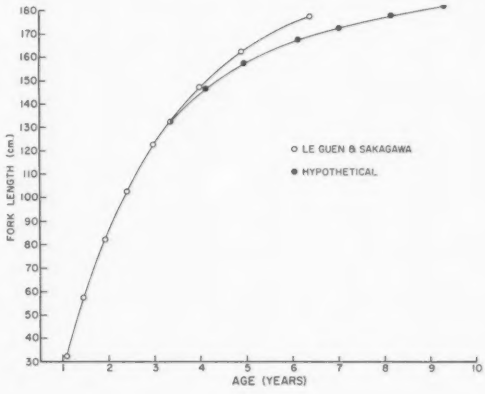

FIGURE 14.—Growth curves of Atlantic yellowfin tuna. Upper curve is from LeGuen and Sakagawa (1973). Lower curve is a modification of the upper curve (see text).

TABLE 6.—Estimates of average weight of catch (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	48.87	47.71	46.73	45.18	44.03	43.14	42.78	42.01	41.41	40.91
117.5	30.6	45.55	44.47	43.56	42.12	41.06	40.24	39.90	39.19	38.61	38.14
112.5	26.9	41.63	40.64	39.80	38.47	37.49	36.72	36.40	35.71	35.15	34.68
107.5	23.5	38.03	37.10	36.32	35.08	34.15	33.42	33.10	32.43	31.87	31.40
102.5	20.4	34.67	33.80	33.07	31.91	31.02	30.31	30.01	29.35	28.79	28.31
97.5	17.6	31.19	30.39	29.71	28.63	27.80	27.12	26.83	26.19	25.65	25.19
92.5	15.0	28.34	27.59	26.96	25.95	25.16	24.53	24.25	23.64	23.12	22.67
87.5	12.7	26.21	25.51	24.91	23.95	23.19	22.58	22.31	21.72	21.21	20.77
82.5	10.7	23.80	23.13	22.57	21.65	20.93	20.34	20.08	19.50	19.00	18.57
77.5	8.9	21.12	20.51	19.98	19.12	18.44	17.87	17.62	17.06	16.58	16.16
72.5	7.3	18.89	18.31	17.82	17.00	16.35	15.81	15.57	15.03	14.56	14.16
67.5	5.9	16.57	16.04	15.58	14.81	14.20	13.68	13.45	12.93	12.48	12.09
62.5	4.7	15.08	14.57	14.13	13.39	12.80	12.29	12.07	11.57	11.13	10.75
57.5	3.7	13.31	12.82	12.40	11.70	11.13	10.64	10.42	9.93	9.50	9.13
52.5	2.8	11.97	11.50	11.10	10.41	9.85	9.37	9.16	8.67	8.25	7.88
47.5	2.1	10.87	10.42	10.02	9.35	8.80	8.33	8.11	7.63	7.21	6.85
42.5	1.5	10.57	10.13	9.73	9.07	8.51	8.04	7.83	7.35	6.93	6.56
37.5	1.0	10.51	10.07	9.67	9.01	8.46	7.98	7.77	7.29	6.87	6.50
32.5	0.7	10.51	10.06	9.67	9.00	8.45	7.98	7.76	7.28	6.86	6.50

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	63.08	60.94	58.99	55.67	53.02	50.93	50.04	48.20	46.76	45.59
117.5	30.6	60.95	58.89	56.65	53.18	50.44	48.28	47.36	45.47	43.98	42.78
112.5	26.9	58.62	56.24	54.09	50.47	47.62	45.38	44.44	42.48	40.94	39.69
107.5	23.5	54.53	51.97	49.68	45.87	42.91	40.61	39.65	37.65	36.10	34.85
102.5	20.4	50.69	48.01	45.65	41.78	38.82	36.55	35.61	33.67	32.18	31.00
97.5	17.6	48.15	45.42	43.03	39.15	36.22	33.99	33.07	31.19	29.74	28.60
92.5	15.0	46.71	43.96	41.55	37.66	34.74	32.53	31.61	29.75	28.32	27.19
87.5	12.7	44.78	41.99	39.57	35.67	32.76	30.55	29.64	27.79	26.37	25.24
82.5	10.7	42.99	40.17	37.73	33.82	30.92	28.72	27.82	25.97	24.55	23.43
77.5	8.9	41.01	38.17	35.71	31.79	28.89	26.71	25.81	23.97	22.55	21.41
72.5	7.3	39.22	36.35	33.88	29.96	27.07	24.89	24.00	22.16	20.74	19.60
67.5	5.9	37.02	34.12	31.65	27.73	24.86	22.69	21.80	19.97	18.55	17.41
62.5	4.7	35.35	32.44	29.96	26.06	23.20	21.05	20.16	18.34	16.93	15.79
57.5	3.7	31.69	28.79	26.34	22.51	19.73	17.65	16.79	15.04	13.68	12.59
52.5	2.8	27.97	25.13	22.75	19.09	16.46	14.52	13.72	12.10	10.86	9.88
47.5	2.1	26.14	23.35	21.02	17.47	14.93	13.07	12.31	10.77	9.60	8.67
42.5	1.5	25.72	22.94	20.63	17.10	14.59	12.74	11.99	10.47	9.31	8.39
37.5	1.0	25.62	22.84	20.54	17.01	14.50	12.66	11.91	10.39	9.23	8.32
32.5	0.7	25.61	22.84	20.53	17.00	14.50	12.65	11.90	10.39	9.23	8.32

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	63.26	61.49	59.84	56.92	54.48	52.45	51.57	49.68	48.15	46.90
117.5	30.6	61.30	59.40	57.62	54.49	51.88	49.72	48.78	46.77	45.16	43.83
112.5	26.9	58.69	56.61	54.69	51.30	48.50	46.19	45.19	43.07	41.37	39.98
107.5	23.5	55.99	53.75	51.68	48.07	45.11	42.70	41.66	39.47	37.72	36.31
102.5	20.4	54.78	52.46	50.33	46.62	43.59	41.13	40.07	37.84	36.07	34.63
97.5	17.6	53.40	51.00	48.79	44.96	41.84	39.30	38.21	35.92	34.10	32.62
92.5	15.0	52.39	49.92	47.65	43.73	40.53	37.94	36.83	34.68	32.62	31.10
87.5	12.7	51.41	48.87	46.54	42.52	39.24	36.59	35.45	33.05	31.13	29.57
82.5	10.7	50.10	47.48	45.07	40.91	37.54	34.80	33.63	31.15	29.16	27.54
77.5	8.9	48.65	45.92	43.43	39.13	35.64	32.82	31.61	29.05	27.00	25.32
72.5	7.3	46.62	43.77	41.16	36.69	33.07	30.15	28.90	26.27	24.16	22.45
67.5	5.9	44.46	41.48	38.78	34.14	30.43	27.44	26.17	23.50	21.38	19.66
62.5	4.7	41.92	38.81	36.01	31.24	27.46	24.46	23.18	20.53	18.44	16.77
57.5	3.7	38.35	35.12	32.23	27.39	23.62	20.67	19.44	16.90	14.94	13.40
52.5	2.8	34.39	31.08	28.17	23.39	19.74	16.96	15.82	13.50	11.75	10.41
47.5	2.1	32.91	29.60	26.69	21.96	18.39	15.68	14.58	12.35	10.69	9.42
42.5	1.5	31.85	28.53	25.64	20.94	17.43	14.78	13.70	11.54	9.93	8.71
37.5	1.0	31.52	28.21	25.31	20.63	17.13	14.50	13.43	11.29	9.70	8.49
32.5	0.7	31.52	28.20	25.31	20.62	17.13	14.50	13.43	11.29	9.70	8.49

TABLE 6.—Estimates of average weight of catch (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

		LONG LINERS									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	59.30	57.92	56.63	54.33	52.38	50.73	50.00	48.41	47.10	46.00
117.5	30.6	57.53	56.05	54.68	52.23	50.16	48.41	47.63	45.96	44.57	43.41
112.5	26.9	55.76	54.18	52.71	50.11	47.91	46.05	45.23	43.45	41.97	40.74
107.5	23.5	54.18	52.51	50.96	48.20	45.87	43.90	43.03	41.14	39.58	38.26
102.5	20.4	52.88	51.13	49.50	46.61	44.16	42.09	41.18	39.19	37.53	36.13
97.5	17.6	52.31	50.51	48.85	45.89	43.38	41.25	40.31	38.26	36.55	35.11
92.5	15.0	51.85	50.02	48.32	45.30	42.74	40.56	39.60	37.49	35.72	34.23
87.5	12.7	51.33	49.46	47.72	44.62	41.98	39.74	38.74	36.55	34.71	33.14
82.5	10.7	50.84	48.93	47.15	43.98	41.27	38.95	37.92	35.65	33.73	32.09
77.5	8.9	50.61	48.68	46.88	43.66	40.91	38.56	37.50	35.19	33.22	31.54
72.5	7.3	50.39	48.44	46.61	43.35	40.56	38.16	37.09	34.72	32.70	30.96
67.5	5.9	50.30	48.34	46.51	43.23	40.41	38.00	36.91	34.52	32.47	30.70
62.5	4.7	50.28	48.31	46.48	43.19	40.37	37.94	36.86	34.45	32.40	30.62
57.5	3.7	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
52.5	2.8	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
47.5	2.1	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
42.5	1.5	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
37.5	1.0	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
32.5	0.7	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56

Figure 15. The values of F of large fish are relatively smaller than those estimated with the original growth curve.

Results of the yield-per-recruit calculations are shown in Table 7. The results indicate that if effort is held constant and size at recruitment is increased to the optimum, less than a 3% increase in yield per recruit would occur. If size at recruitment is constant and effort is doubled, yield per recruit would increase by about 28% which is considerably more than when the original growth curve is used. If size at recruitment is increased to 77.5 cm and effort doubled, a 44% increase in yield per recruit would occur.

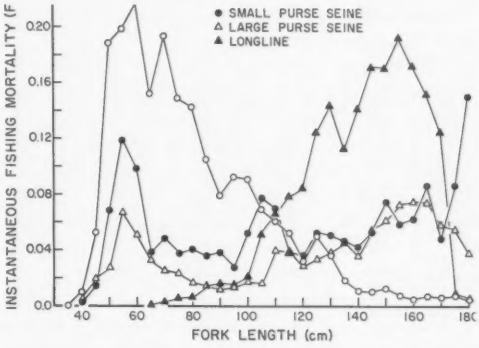

FIGURE 15.—Estimates of size-specific F when its initial value is 0.2 and using the modified growth curve.

TABLE 7.—Estimates of yield per recruit (kg) for the entire fishery when $M = 0.8$, initial $F = 0.2$, and hypothetical growth curve is used.

		ENTIRE FISHERY									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.80	1.48	2.06	2.99	3.70	4.24	4.47	4.95	5.32	5.61
117.5	30.6	0.84	1.55	2.15	3.12	3.85	4.41	4.65	5.13	5.50	5.79
112.5	26.9	0.88	1.62	2.25	3.25	4.00	4.58	4.82	5.30	5.67	5.97
107.5	23.5	0.92	1.70	2.35	3.39	4.15	4.74	4.98	5.46	5.83	6.11
102.5	20.4	0.96	1.76	2.43	3.49	4.27	4.85	5.09	5.57	5.93	6.21
97.5	17.6	0.98	1.80	2.49	3.56	4.35	4.93	5.17	5.64	5.99	6.25
92.5	15.0	1.00	1.84	2.53	3.62	4.40	4.98	5.21	5.68	6.01	6.26
87.5	12.7	1.02	1.87	2.57	3.66	4.44	5.01	5.24	5.69	6.01	6.25
82.5	10.7	1.04	1.89	2.60	3.69	4.47	5.03	5.25	5.69	5.99	6.21
77.5	8.9	1.05	1.92	2.63	3.72	4.48	5.03	5.24	5.65	5.93	6.12
72.5	7.3	1.07	1.94	2.66	3.74	4.48	5.01	5.21	5.59	5.84	6.01
67.5	5.9	1.08	1.96	2.68	3.74	4.47	4.96	5.15	5.49	5.70	5.83
62.5	4.7	1.09	1.98	2.69	3.74	4.44	4.91	5.08	5.39	5.57	5.66
57.5	3.7	1.11	1.99	2.69	3.71	4.37	4.80	4.95	5.20	5.32	5.37
52.5	2.8	1.11	1.99	2.69	3.67	4.28	4.66	4.79	4.98	5.05	5.05
47.5	2.1	1.12	1.99	2.68	3.63	4.21	4.55	4.66	4.81	4.84	4.81
42.5	1.5	1.12	1.99	2.67	3.62	4.18	4.51	4.61	4.75	4.77	4.73
37.5	1.0	1.12	1.99	2.67	3.61	4.18	4.50	4.60	4.73	4.75	4.71
32.5	0.7	1.12	1.99	2.67	3.61	4.17	4.50	4.60	4.73	4.75	4.70

Sensitivity of Results to Errors in Estimates of Natural Mortality

Size-specific values of F were estimated using values of M of 0.6 and 1.0 and an initial value of $F = 0.2$. The results are compared to size-specific F when $M = 0.8$ in Figure 16. Although the absolute values differ considerably, the same general trends appear in each curve. The ratio of F/M varies about threefold.

Results of yield-per-recruit calculations are shown in Tables 8 and 9 and Figures 17 and 18. There is a steeper horizontal gradient when $M = 1.0$ and a steeper vertical gradient when $M = 0.6$ than when $M = 0.8$. That is, yield per recruit is more sensitive to changes in effort

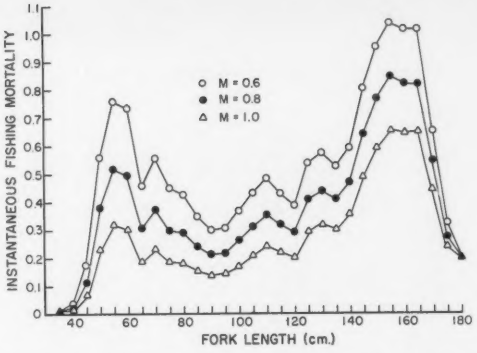

FIGURE 16.—Estimates of size-specific F when its initial value is 0.2 and using values for M of 0.6, 0.8, and 1.0.

TABLE 8.—Estimates of yield per recruit (kg) for the entire fishery when $M = 0.6$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

		ENTIRE FISHERY									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	3.52	5.82	7.34	9.07	9.93	10.39	10.55	10.81	10.98	11.10
117.5	30.6	3.61	5.94	7.47	9.18	10.00	10.43	10.58	10.81	10.95	11.04
112.5	26.9	3.70	6.06	7.58	9.26	10.04	10.44	10.56	10.76	10.86	10.92
107.5	23.5	3.79	6.16	7.68	9.30	10.03	10.38	10.48	10.63	10.70	10.72
102.5	20.4	3.85	6.24	7.74	9.31	9.98	10.28	10.36	10.47	10.49	10.48
97.5	17.6	3.90	6.28	7.77	9.28	9.91	10.16	10.22	10.28	10.27	10.22
92.5	15.0	3.93	6.31	7.77	9.24	9.82	10.03	10.07	10.09	10.04	9.97
87.5	12.7	3.95	6.33	7.77	9.18	9.70	9.87	9.90	9.87	9.79	9.68
82.5	10.7	3.97	6.33	7.74	9.09	9.55	9.66	9.66	9.58	9.45	9.31
77.5	8.9	3.99	6.33	7.70	8.95	9.33	9.38	9.35	9.20	9.01	8.82
72.5	7.3	4.00	6.31	7.63	8.79	9.08	9.06	8.99	8.78	8.54	8.30
67.5	5.9	4.01	6.27	7.53	8.57	8.75	8.64	8.54	8.25	7.94	7.65
62.5	4.7	4.01	6.23	7.44	8.37	8.47	8.29	8.16	7.80	7.45	7.13
57.5	3.7	4.00	6.15	7.28	8.05	8.01	7.73	7.55	7.11	6.70	6.33
52.5	2.8	3.98	6.06	7.10	7.70	7.54	7.16	6.95	6.43	5.97	5.56
47.5	2.1	3.96	5.99	6.96	7.45	7.20	6.75	6.52	5.95	5.46	5.04
42.5	1.5	3.95	5.96	6.92	7.37	7.09	6.62	6.38	5.80	5.30	4.87
37.5	1.0	3.95	5.96	6.90	7.35	7.06	6.59	6.35	5.77	5.26	4.83
32.5	0.7	3.95	5.96	6.90	7.34	7.06	6.59	6.34	5.76	5.26	4.83

TABLE 9.—Estimates of yield per recruit (kg) for the entire fishery when $M = 1.0$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

		ENTIRE FISHERY									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.66	1.18	1.62	2.26	2.72	3.06	3.19	3.47	3.67	3.84
117.5	30.6	0.69	1.24	1.68	2.36	2.83	3.18	3.32	3.60	3.81	3.98
112.5	26.9	0.72	1.29	1.76	2.45	2.94	3.30	3.45	3.74	3.96	4.13
107.5	23.5	0.75	1.35	1.83	2.55	3.06	3.42	3.57	3.87	4.09	4.27
102.5	20.4	0.77	1.39	1.89	2.63	3.15	3.52	3.67	3.97	4.20	4.37
97.5	17.6	0.79	1.43	1.93	2.69	3.21	3.59	3.74	4.04	4.27	4.44
92.5	15.0	0.81	1.45	1.97	2.73	3.26	3.64	3.79	4.09	4.31	4.48
87.5	12.7	0.82	1.47	1.99	2.76	3.29	3.67	3.82	4.12	4.34	4.50
82.5	10.7	0.83	1.49	2.02	2.79	3.32	3.70	3.85	4.14	4.35	4.51
77.5	8.9	0.85	1.51	2.05	2.82	3.35	3.72	3.86	4.14	4.34	4.49
72.5	7.3	0.86	1.53	2.07	2.84	3.36	3.72	3.86	4.13	4.32	4.45
67.5	5.9	0.87	1.55	2.09	2.86	3.37	3.72	3.85	4.10	4.27	4.38
62.5	4.7	0.88	1.56	2.10	2.86	3.36	3.70	3.82	4.06	4.21	4.31
57.5	3.7	0.89	1.57	2.11	2.86	3.34	3.65	3.76	3.97	4.09	4.16
52.5	2.8	0.90	1.58	2.11	2.84	3.30	3.58	3.68	3.85	3.94	3.99
47.5	2.1	0.90	1.58	2.11	2.82	3.26	3.52	3.61	3.76	3.83	3.85
42.5	1.5	0.90	1.58	2.10	2.81	3.24	3.50	3.59	3.73	3.79	3.80
37.5	1.0	0.90	1.58	2.10	2.81	3.24	3.50	3.58	3.72	3.78	3.79
32.5	0.7	0.90	1.58	2.10	2.81	3.24	3.50	3.58	3.72	3.78	3.79

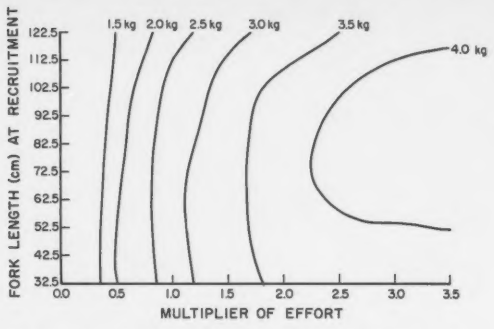

FIGURE 17.—Yield-per-recruit isopleths for the entire Atlantic yellowfin tuna fishery with $M = 1.0$.

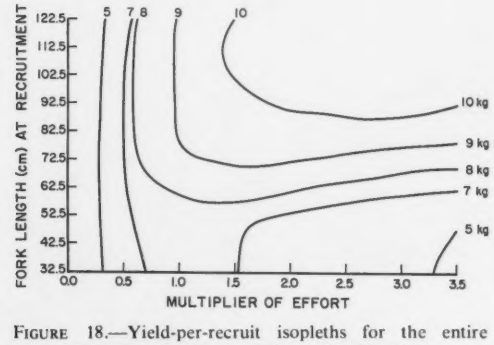

FIGURE 18.—Yield-per-recruit isopleths for the entire Atlantic yellowfin tuna fishery with $M = 0.6$.

when $M = 1.0$ and more sensitive to changes in size at recruitment when $M = 0.6$ than when $M = 0.8$. When $M = 1.0$ and effort is constant an increase in size at recruitment to 77.5 cm does not change yield per recruit. However, when $M = 0.6$, the same change in size at recruitment causes a 22% increase in yield per recruit. When $M = 1.0$ and size at recruitment is held constant, a doubling of effort causes a 29% increase in yield per recruit. When $M = 0.6$, the same change causes a 14% decrease in yield per recruit. When $M = 1.0$ and size at recruitment is increased to 77.5 cm, a doubling of effort causes a 39% increase in yield per recruit. When $M = 0.6$, the same changes cause a 27% increase in yield per recruit.

DISCUSSION

The use of results of our study must be based on three further assumptions: (1) the composition of the fleet will not change; (2) either the gear is currently dispersed so that all qualitative characteristics of the population are available to capture by each gear, or that the dispersal of gear as it now stands will not change; and (3) recruitment is constant.

Relation Between Composition of Fleet and Optimum Size at Recruitment

The preceding text has assumed that the composition of the fleet remains constant. The history of the fishery reveals that the composition has been a very dynamic process and there is no reason to believe that it will not continue to be. Since each fishing gear has a different curve of size-specific F, changes in the fleet composition will cause changes in size-specific F for the entire fleet. These changes will cause changes in the yield-per-recruit isopleths.

To illustrate the influence of changes in fleet composition on management strategy, the optimum size at recruitment was estimated for 441 combinations of baitboat and longline effort. For simplicity, effort of purse seiners is not included, i.e., we excluded two variables—small and large purse seiners. Multipliers of effort for each gear ranged from 0 to 2.0 with increments of 0.1.

The results (Table 10) show a considerable range in the estimates of optimum size at recruitment and that minimum size regulations must be adjusted to changes in the composition of the fleet to maintain maximum yield per recruit. As an example, with a 1.0 level of effort by both gears, the minimum size should be about 72.5 cm. If this were instituted as a minimum size regulation, the bait boat effort might decline to about 0.2 because of the extreme loss of catch. The minimum size, therefore, should be lowered to 67.5 cm. Now the longline effort might increase by about 80% due to the decrease in competition from bait boats—the minimum size should be increased to 77.5 cm. Finally, suppose an innovation occurs in bait fishing such that non-nominal effort again increases to about 0.7—the minimum size should be raised further to about 82.5 cm. These changes could occur slowly allowing for a smooth transition of the minimum size regulations. When economics are involved, however, the changes might be precipitous causing the confusion in the above example. If the possible changes in

TABLE 10.—Optimum size (cm) at recruitment for 441 combinations of multipliers of effort by bait boats and longliners.

Longline multiplier	Bait boat multiplier																				
	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
0	32.5	32.5	32.5	32.5	32.5	32.5	37.5	37.5	42.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5
0.1	32.5	32.5	32.5	37.5	37.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5
0.2	32.5	37.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5
0.3	32.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5
0.4	32.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5
0.5	32.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5
0.6	32.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5
0.7	32.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5
0.8	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5
0.9	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5
1.0	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5
1.1	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5
1.2	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.3	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.4	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5
1.6	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5
1.7	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
1.8	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
1.9	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
2.0	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5

composition of both small and large purse seiners are included, the attempts to achieve some reason in the minimum size regulation based on maximum yield per recruit can become quite unwieldly.

Dispersion of Gear and Yield Per Recruit

The second assumption could be important. For example, in the eastern Pacific yellowfin tuna fishery effort has expanded farther offshore. Evidence suggests that larger fish were farther offshore and were not previously fully available to the fishery. A possible consequence of this phenomenon is a change in yield per recruit. Upon analysis of the data, the Inter-American Tropical Tuna Commission concluded, however, that the possible increase is minor (Joseph, pers. commun.). The surface gears have been fishing quite close to shore in the Atlantic. The possibility of offshore dispersal of the surface fleets and the effects of such a change on yield per recruit are unknown.

Interaction Between Minimum Size and Catch Quota Regulations

If recruitment is not constant, then the interaction between minimum size and catch quota regulations should be examined. Catch quotas are frequently based on assessments of the maximum sustainable average yield (MSAY), usually through a production model type analysis. The shape of the total yield curve, however, may be strongly dependent on the age at recruitment, t_r'. Therefore, the interaction between the two types of regulation should be examined before a singular action is taken. As an illustration, consider a population consisting of six age-groups with the growth curve and natural mortality coefficient ($M = 0.8$) similar to that of the Atlantic yellowfin tuna fishery, and assume also that recruitment is knife-edged at 19 mo. Figure 19 (lower curve) shows the total annual yield as a function of fishing mortality with an assumed arbitrary stock-recruitment function. Assume further that the fishery is operating at an $F = 1.0$. The yield per recruit at $F = 1.0$ and $t_r' = 19$ mo is 5.39, but the maximum yield per recruit is 6.11 at $t_r' = 27$ mo. If singular action were taken to increase t_r' to 27 mo, the upper total yield curve in Figure 19 would result. Not only did the yield per recruit increase, but so did the total yield at $F = 1.0$. In addition, the MSAY increased, but occurs at a much higher value for F. A phenomenon such as this may have occurred inadvertantly in the eastern tropical Pacific with the introduction of purse seiners which gave a better yield per recruit than the existing bait boats (Joseph, 1970).

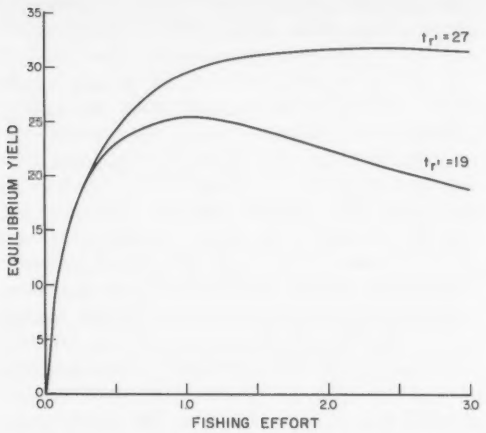

FIGURE 19.—Annual equilibrium yield as a function of fishing effort at two different ages at recruitment, t_r'.

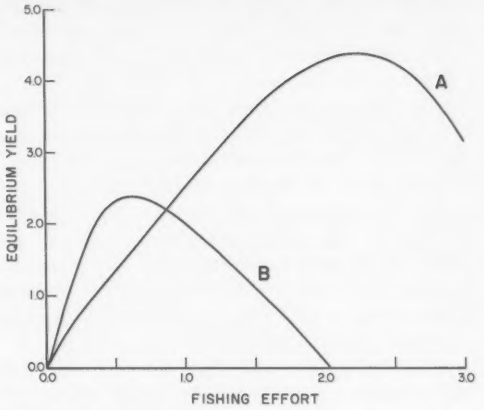

FIGURE 20.—Annual equilibrium yield as a function of fishing effort at two different ages at recruitment (see text).

The above result of singular action on the minimum size regulation resulted in a fortuitous increase in total yield and MSAY. This result may not always occur, however. Consider that if the fishery were operating with t_r' at 27 mo and $F = 0.2$, then the yield per recruit would be 2.77. The optimal yield per recruit is 3.02 at a t_r' of 19 mo. If singular action were taken to lower the t_r' to 19 mo, a slight loss of total yield would occur even with the improved yield per recruit. Even more disconcerting would be the loss in potential MSAY of 28%. The fishery would be suboptimized in a sense. Since the MSAY is usually estimated from a time series of catch and effort data, the actual potential which could have been realized had t_r' remained at 27 mo would likely be underestimated. It is likely that yield per recruit studies would continue as the fishery developed effort beyond $F = 0.2$, such that eventually the upper curve might be attained; this is because the optimal age at recruitment increases asymptotically as F increases. The low initial forecasts of MSAY, however, could hamper development of the fishery.

An even worse consequence of singular action on yield per recruit is illustrated in Figure 20. Assume the fishery is operating at about 0.6 unit of effort with an age at recruitment such to obtain curve A, but the yield per recruit is adjusted to maximal for the age at recruitment giving curve B. The actual MSAY of curve A might never be realized since the maximum equilibrium yield in curve B is also at 0.6 unit of fishing effort. This case represents true suboptimization.

CONCLUSIONS

Although there are some uncertainties in our knowledge of the parameters that enter into calculations of yield per recruit of yellowfin in the Atlantic, it is possible to come to some conclusions from our results.

The least amount of data and assumptions is involved in the simplified Beverton and Holt method. Results from this method (Table 1) show that, in all but a few extreme cases in a wide range of growth and mortality parameter values, an increase in the effective minimum size would result in an increase in yield per recruit. However, our most reasonable estimates of the parameters indicated that at the current level of fishing, an increase in the effective minimum size could only result in about an 8% increase in yield per recruit. We conclude that even if the quality of our data is poor an increase, probably minor, in yield per recruit of Atlantic yellowfin would occur if the effective minimum size is increased and if it is assumed that small yellowfin tuna were not dumped.

We next assumed that our most reasonable estimate of growth, constant Z, and effective minimum size are correct and constructed yield-per-recruit isopleths with the Ricker method for

several values of natural mortality. The results (Figures 1-3) indicated that yield per recruit would increase from 0 to 20% if effective minimum size is increased and effort remains constant. Again, our most reasonable estimate of the increase is only 8%. The results also indicate that little if any increase in yield per recruit would occur if fishing effort is doubled and effective minimum size is unchanged. However, if the effective minimum size is increased and effort is doubled, a modest (20 to 40%) increase in yield per recruit could occur. All these results again assume that there would be no dumping of small yellowfin tuna.

We finally assumed that the available data are accurate enough to also make reasonably accurate estimates of size-specific F. When using our most reasonable parameter estimates and holding effort constant, an increase in size at recruitment to 55 cm (3.2 kg) would obtain a 3.9% increase in yield per recruit and to 77.5 cm (8.9 kg) would cause less than a 10% increase in yield per recruit. Increasing the size at recruitment to 55 cm with $M = 0.6$ would cause a 7% increase in yield per recruit, but with $M = 1.0$ only a 1% increase would occur. Increasing the size at recruitment to 77.5 cm with $M = 0.6$ would increase yield per recruit by 22%, but with $M = 1.0$ no increase would occur. When size at recruitment is held constant and fishing effort is doubled, our best estimate of the change in yield per recruit is a 6% increase. Our estimates ranged from a 14% decrease to a 29% increase. It seems safe to agree with the report of the Abidjan meeting that if conditions remain constant, there is little to be gained on a yield-per-recruit basis from increases in fishing effort. With a doubling of fishing effort and an increase in size of recruitment to 55 cm, our most reasonable estimate is a 15% increase in yield per recruit, with a range of a 1% decrease to a 35% increase. When size at recruitment is increased to 77.5 cm and fishing effort is doubled, our most reasonable estimate of the change in yield per recruit is a 30% gain; however, the estimates range from 27 to 44%. Thus it appears that if it is possible to increase the size at recruitment, a doubling of effort would produce a modest increase in yield per recruit. These results, it must be noted, assume that small yellowfin tuna are not dumped.

It is interesting to note that the same general conclusions would be made using either the knife-edged recruitment or size-specific F approaches. The size-specific F approach, in addition, allows us to examine more precisely the effects of an absolute minimum size regulation and the effects on each gear. The general conclusions from both aspects of this study also agree fairly well with those of Joseph and Tomlinson (1972, see footnote 4). It is not surprising, however, that results from the size-specific F approach agree with theirs because they used similar methodology and data. Both estimates suggest that under present conditions the fishery is near the point of maximum yield per recruit.

Specifically addressing the recommendations outlined in the introduction section of this paper for considering a minimum size between 3.2 and 10 kg, we offer the following results based on our most reasonable parameter estimates:

1. Minimum size limit 55 cm (3.2 kg):
   a) Current levels of fishing mortality:
      i) No dumping results in a 4% increase in landed yield per recruit
      ii) 100% dumping results in a 3% decrease in landed yield per recruit
   b) Doubling fishing mortality:
      i) No dumping results in a 15% increase in landed yield per recruit
      ii) 100% dumping results in a 1% increase in landed yield per recruit

2. Minimum size limit 77.5 cm (8.9 kg):
   a) Current levels of fishing mortality:
      i) No dumping results in a 9% increase in landed yield per recruit
      ii) 100% dumping results in a 13% decrease in landed yield per recruit
   b. Doubling fishing mortality:
      i) No dumping results in a 31% increase in landed yield per recruit
      ii) 100% dumping results in a 16% decrease in landed yield per recruit.

The 55-cm (3.2 kg) minimum size limit would likely be of more benefit to the tuna fishery than the larger minimum size limit of 77.5 cm (8.9 kg) since less dumping would occur. Therefore, there would likely be, on the average, an increase in landed yield per recruit at the current or greater levels of fishing mortality; whereas, if a larger size limit were adopted, there would likely be, on the average, a decrease in landed yield per recruit at current levels of fishing

mortality and less of an increase (perhaps even a decrease) in landed yield per recruit than with the 55-cm (3.2 kg) minimum size and an increase in fishing mortality.

The results of this paper were obtained using reasonable assumptions and all available data on Atlantic yellowfin tuna. As we increased the number of assumptions we increased the number of conclusions. We think that it is unlikely that use of tecnhiques not used in this paper would result in conclusions that are significantly different from ours. That is, an increase in effective minimum size would result in a minor increase in yield per recruit, an increase in effort without increasing effective minimum size would not appreciably increase yield per recruit, and an increase in effective minimum size and effort would result in modest gains in yield per recruit. We wish to emphasize that these conclusions are based on a number of assumptions. We consider the assumptions reasonable, but because they are assumptions any management decisions, including the decision of taking no action, should be followed with careful evaluation of the results.

ACKNOWLEDGMENTS

We are indebted to James Joseph and Patrick Tomlinson of the Inter-American Tropical Tuna Commission for their useful comments on this paper. This study would not have been possible without the many valuable contributions of data and ideas by scientists of the nations that participate in the International Commission for the Conservation of Atlantic Tunas.

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SYSTEMATICS AND DISTRIBUTION OF THE FOUR SIBLING SPECIES COMPRISING THE GENUS *PONTELLINA* DANA (COPEPODA, CALANOIDA)

A. FLEMINGER AND K. HULSEMANN[1]

ABSTRACT

A global-scale study on systematics and distribution of the epipelagic copepod genus *Pontellina* (Family Pontellidae) was carried out on materials sorted from about 2,000 zooplankton samples collected at stations scattered throughout the circumglobal warm-water belt. Four distinctive species were found and described, three being new to science.

Each species was examined for evidence of conspicuous polytypy and geographical variation. Morphology and geographical distribution were utilized comparatively to perceive relationships that would shed light on the nature of selection pressures operating on external morphology. Morphology and distribution were also considered to determine phylogenetic relationships within the genus.

The geographic distribution of the four species was considered relative to major near-surface hydrographic features characterizing tropical and subtropical latitudes and especially the occurrence of eutrophic and oligotrophic areas in each ocean.

Sets of similarly collected, quantitative samples were used to determine the relative abundance of each species, and co-occurrences among the species were tested by recurrent group analysis. The trophic role of each species was considered and conclusions tested by a limited series of observations on stomach contents.

Geographical perspective, too often absent from studies on marine plankton, is a powerful tool for dealing with sibling species. Evidence of reproductively isolated populations that are morphologically similar in planktonic calanoids and other zooplankton as well has been presented in a number of studies combining geographical distribution and morphology (e.g., Schmaus, 1917; Johnson, 1935; Bowman, 1955, 1967; Brodsky, 1959; Foxton, 1961; Jones, 1966; Fontaine, 1967; Fleminger, 1967b; Frost and Fleminger, 1968; Mullin, 1969; Jaschnov, 1970). Our resolution of the sibling species comprising the genus *Pontellina* Dana is offered as an additional example.

In contrast to the 22 nominal species by our count comprising *Pontellopsis* Brady, the pontellid genus most similar in morphology, *Pontellina* has been universally regarded as monotypic since Giesbrecht's (1892) monumental review of planktonic marine copepods. Mori (1937) presented evidence of polytypy in *Pontellina* with his description of a unique male distinguished by an unusual chela. Apparently influenced by Sewell's views on copepod ontogeny (1929, 1932), Mori ascribed the specimen taken off Japan to *plumata*, suggesting that it represented the fully mature state and that previous descriptions of the *plumata* male were based on incompletely mature specimens. Our study was prompted by the appearance of other seemingly minor morphological features distinguishing adult individuals of both sexes that correlated with indications of distinctive geographical distributions among the observed forms.

In this paper we redefine the genus and describe its four species. The distribution of each species is considered in the context of our geographical records. Distribution is also discussed with respect to morphological similarities among the species and relationships to general oceanic circulation. Detailed considerations and views regarding environmental conditions that shape these distributions and the circumstances yielding the contemporary *Pontellina* speciation pattern will be presented separately elsewhere.

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MATERIALS AND METHODS

Materials

Plankton samples examined for the genus *Pontellina* in the course of this study were obtained from three major sources: the zooplankton collections of Scripps Institution of Oceanography, R. Scheltema's collection of Atlantic zooplankton maintained at the Woods Hole Oceanographic Institution, and quantitative sortings of *Pontellina* from the International Indian Ocean Expedition plankton collections, processed and furnished by the Indian Ocean Biological Centre, Cochin, India. Additional collections or specimens were obtained with the kind cooperation of the National Marine Fisheries Service; the U.S. Naval Oceanographic Office; T. K. S. Björnberg, University of São Paulo, Brazil; A. DeDecker, Division of Sea Fisheries, Cape Town, Republic of South Africa; B. Kimor, Israel Oceanographic and Limnological Research Ltd., Haifa, Israel; J. E. H. Legaré, Instituto Oceanográfico, Cumaná, Venezuela; D. J. Tranter, CSIRO, Cronulla, Australia.

Geographical distribution of the samples is shown in Figure 1a, and the localities yielding *Pontellina* are listed by species in Table 1. These collections broadly outline most major sectors of the Pacific, Indian, and Atlantic Oceans, the South Atlantic being the notable omission. Most of the samples were taken with open conical plankton nets ½ to 1 m in diameter at the mouth. Nets were towed obliquely, vertically, or horizontally between the surface and 200 m of depth. Stations were occupied irrespective of time of day or cloud cover.

Sample Analysis

Plankton samples were examined in rectangular plastic trays (5 × 7.5 × 1 cm) at 16 × magnification with the aid of a stereomicroscope. The entire sample was scanned if the settling volume did not exceed 20 cc. Otherwise volumetric subsamples were drawn, generally with the aid of a 10-cc piston pipette, after standardizing the total volume and stirring vigorously. Usually more than 2% of the total sample was examined, the actual percentage varying inversely with the size of the original sample.

Estimates of abundance and frequency of occurrence were obtained from particular sets of quantitative samples (Figure 1b) selected for homogeneity of sampling. In the case of Pacific zooplankton samples collecting procedures followed standard CalCOFI (California Cooperative Oceanic Fisheries Investigations) sampling practices (cf. Smith, 1971). The Indian Ocean samples (Figure 1b) are a composite of quantitative Indian Ocean Standard Net tows (Currie, 1963) obtained by various participants in the International Indian Ocean Expedition. Preliminary quantitative processing of these samples was carried out by the Indian Ocean Biological Centre, Cochin, India (Tranter, 1969). The Centre provided us with specimens of *Pontellina* sorted from known fractions of the original samples. Standard quantitative sampling from the Atlantic Ocean was unavailable to us.

Specimen Analysis

For routine examinations specimens were mounted loosely in a drop of glycerol. To enhance examination of fine denticles and spines, soft tissue was removed by warming specimens in a 10% aqueous solution of KOH at about 90°C for 1 to 2 h. After a brief rinse in distilled water the cuticle was transferred to 35% ethanol, then to 70% ethanol for 1 min and then stained in a solution of 1% Chlorazol Black E dissolved in 70% ethanol. Intensive staining usually requires not more than ½ min and should be followed immediately by a 1-min rinse in distilled water.

Examinations and dissections were carried out under stereomicroscopes at 12× to 100× magnification and under compound microscopes at various magnifications up to 600×. All drawings were made with the aid of a compound microscope equipped with a drawing attachment.

Several females and males of each species were studied under a scanning electron microscope after preparation by the critical point drying method (Cohen, Marlow, and Garner, 1968).

Measurements

For each species intact specimens with a reasonably straight urosome were chosen at random from localities scattered over the entire

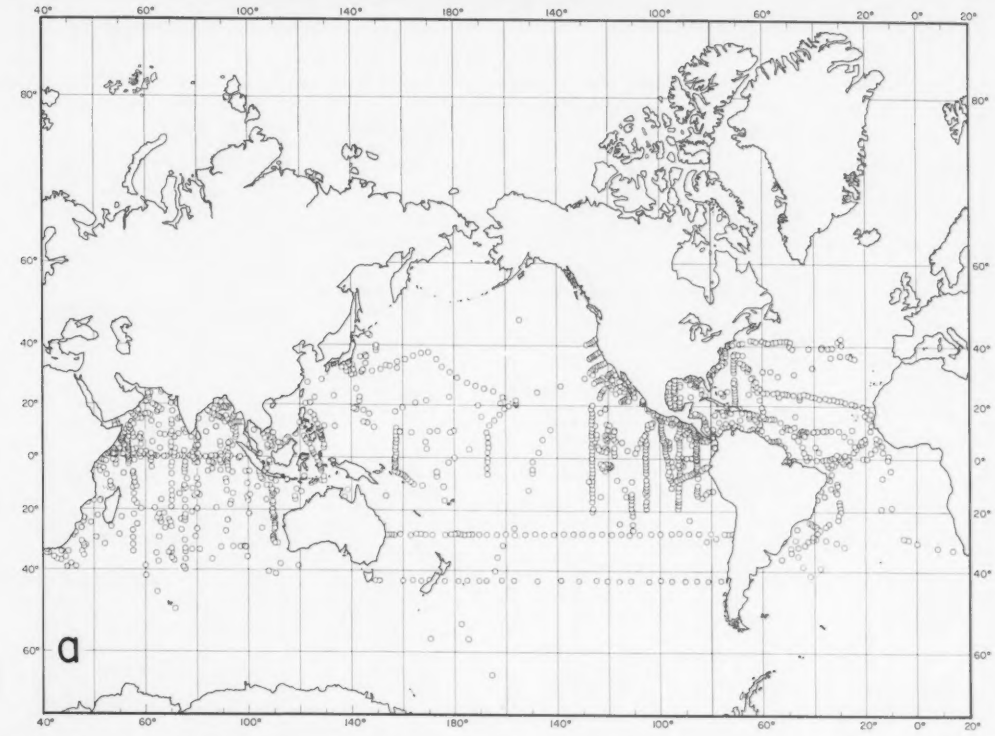

FIGURE 1a.—Geographical distribution of sampling stations. Each open circle represents one or more samples. Overlapping stations and replicate sampling are omitted for the purpose of clarity. Areas intensively surveyed are shown symbolically as evenly spaced grid.

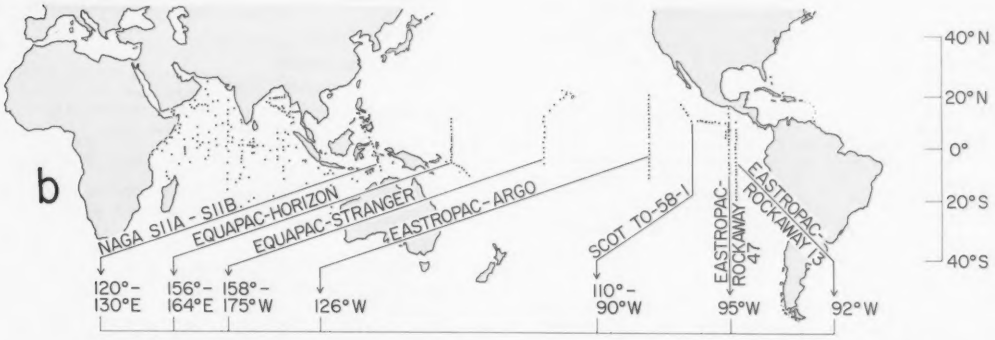

FIGURE 1b.—Distribution and identification of sets of quantitative zooplankton samples used to estimate the frequency of *Pontellina* in the Pacific Ocean. Sets were selected for similarity of sampling; i.e., each set obtained by the same procedures and stations occupied in a closely ordered sequence during the same cruise. Dots indicate the sampling localities. Indian Ocean localities represent Indian Ocean Standard Net samples collected during the International Indian Ocean Expedition that were examined quantitatively for *Pontellina* in the course of this study. See Table 14 for summary of sampling data and Materials and Methods for analytical details.

TABLE 1.—Localities yielding *Pontellina* listed by species.

Location and station		Source of collecting data[1]
PONTELLINA PLATYCHELA		
Atlantic Ocean:		
RV *Alaska* 4:	29, 46.	H
Amazon Exp.:	17, 19.	B
RV *Atlantis II*-20:	2, 6, 9, 10, 12, 14, 15, 16, 24, 25, 26, 27, 28, 29, 31, 34, 35, 38, 39, 42, 49, 50, 56, 60.	F
-31:	25, 38, 40, 41, 43, 47, 48, 49, 50, 54, 55, 56, 57.	
-32:	60, 61, 84, 85, 86, 88, 89, 90, 94A, 98, 108, 110, 112.	
Cato 6 Exp.:	34 (26°11'S 38°46'W), 46 (34°37'S 47°58'W).	
RV *Chain* 35:	19, 29, 33, 39, 43.	F
RV *Chain* 60:	13, 16.	
La Creuse Exp.:	4, 5, 7, 10.	B
Lusiad VII Exp.:	69 H-4, 73 H-5, 79 (00°56'N 11°29'W), 80 H-12, 81 H-13.	A
RV *Oregon:*	1289 (17°10'N 74°20'W), 1291 (17°50'N 72°00'W), 1292 (18°08'N 74°35'W), 1293 (19°55'N 74°10'W), 1294 (19°45'N 74°45'W).	
RV *Thomas Washington:*	8.	B
10°29'N 64°12'W (Cumaná, Venezuela).		
PONTELLINA PLUMATA		
Atlantic Ocean:		
RV *Alaska* 1:	29.	H
2:	46, 56.	
4:	10, 29, 40, 42, 46.	
5:	42.	
Amazon Exp:	19, 20.	B
RV *Atlantis II*-13:	9, 35, 44, 48.	F
-20:	2, 22.	
-31:	2, 5, 6, 7, 8, 9, 11, 13, 15, 17, 18, 21, 23, 24, 25, 26, 28, 29, 38, 44, 57.	
-32:	61, 62, 63, 64, 66, 67, 68, 72, 73, 74, 87, 118D, 119.	
Björnberg:	M 242 (11°24'S 33°19'W).	
Cato 6 Exp.:	33 (25°16'S 49°01'W), 34 (36°11'S 38°46'W), 36 (30°06'S 39°21'W), 39 (30°26'S 35°20'W), 40 (30°56'S 31°21'W), 41 (32°28'S 28°17'W), 48 (30°10'S 39°23'W), 49 (25°50'S 39°24'W), 50 (24°33'S 41°02'W).	
RV *Chain* 49:	3, 5, 8, 9, 10, 11, 14, 15, 16, 17, 19, 20, 21, 22, 23, 26, 27.	F
60:	17.	
Cyprus:	10-20 (off coast of Israel).	
RV *Delaware*:	7, 19, 20, 25.	
La Creuse Exp.:	3, 4, 5, 7, 10.	B
Lusiad VII Exp.:	21 (30°23'S 02°47'W), 24 (30°09'S 04°42'W), 52 (19°13'S 13°44'W).	
N-3 Cruise:	4 (30°55'N 79°21'W).	
RV *Oregon:*	1291 (17°50'N 72°00'W), 1292 (18°08'N 74°35'W), 1294 (19°45'N 74°45'W).	
RV *Theodore N. Gill* 2:	41.	G
5:	3, 4.	
7:	4, 5.	
8:	5, 9.	
Pacific Ocean:		
Aries I Exp.:	30 (09°20'S 127°05'W).	
Bonacca Exp.:	22.	A
CalCOFI Cruise 5804:	80.110, 60.110, 100.80.	E
5810:	100.70, 120.90.	
5901:	100.70.	
Capricorn Exp.:	1, 2, 3, 28, 29, 30, 31, 32, 33, 35.	A
Circe I Exp.:	3, 4.	B
Circe II Exp.:	9, 11, 12, 13, 14.	
RV *David Starr Jordan* 57:	025 (10°30'N 119°43.5'W), 076 (03°20'N 119°42'W), 116 (7°30'N 119°43.5'W), 123 (07°00'N 120°40'W), 130 (09°31'N 120°39'W), 132 (09°45'N 120°12'W).	
60:	071 (02°00'N 117°17'W), 122 (04°00'N 116°41'W), 134 (07°05'N 116°58'W).	
EASTROPAC Exp.:		
RV *Argo* 11:	197, 215, 234, 242, 250, 266, 282, 287, 291, 299, 303, 308, 320, 328.	D
RV *David Starr Jordan* 12:	053, 059, 063.	D
RV *Rockaway* 13:	056.	D
EQUAPAC Exp.:		
RV *Horizon*:	19, 20, 21, 22, 23, 24, 25, 26, 27, 29, 30, 31, 32, 34, 35, 36, 37, 38, 39, 40, 41.	A
RV *Stranger:*	3, 5, 11, 15, 17, 19, 21, 23.	A
Monsoon Exp.:	1, 2, 3, 4, 5, 7, 35, 37, 38, 39, 40.	A
Muddauber Exp.:	TDS-86.	B
Naga Exp. S11A:	160, 164, 169, 169A.	B
S11B:	5, 10, 16, 17, 20, 24, 27, 29, 31, 36, 38, 41, 50, 58, 62, 66, 78, 86.	
NAVOCEANO RV *Hunt* 1968:	12, 14.	B
1969 (Apr.):	8, 31-6.	
1969 (May):	9.	
1969 (Oct.):	3.	
1969 (A-14):	6, 16.	
NAVOCEANO RV *Silas Bent:*	1-10, 1-11, 1-12, 1-16, 1-20.	B
Piquero IV Exp.:	12, 16, 17.	B
V Exp.:	40D, 43D, 44, 45D, 46, 47N, 47D, 48, 49, 50D.	
Scan IV Exp.:	1, 2, 35D, 6.	B
V Exp.:	5.	
Scorpio II Exp.:	92, 96, 98, 112, 114, 118, 120, 122, 138, 140, 144, 146, 148, 152, 154, 160, 164, 166, 168, 170, 172, 174, 176, 180, 182.	B
Shellback Exp.:	47, 51, 103.	A
TO-58-1 Cruise (Scot):	27, 29, 37, 56B.	B
TO-60-2 Cruise (Step 1):	62.	B
RV *Townsend Cromwell* 51:	064 (03°30'S 120°45'W), 085 (02°29'N 120°49'W).	
TRANSPAC Exp.:	85A, 87A, 87B, 89A, 92A, 92B, 94A, 96A, 98A, 98B, 100A, 102A, 106A, 108A, 110A, 112A, 118A, 118B, 122A, 126A, 126B, 132A, 134A, 142A, 143A.	A
Troll Exp.:	24, 24A, 25, 25A, 27, 27A, 28, 28A, 29, 30A, 31, 31A, 32, 32A, 33, 35.	A
32°15'N 117°16'W (15-VIII-1962).		
Indian Ocean:		
Circe II Exp.:	Camera 3.	B
III Exp.:	22, 25, 27, 28, 29, 38.	
RV *Diamantina:*	3/93/63 (27°30'S 110°00'E).	
Dodo VI Exp.:	13, 65, 70, 74, 81.	A
RV *Gascoyne:*	G1/5/63 (27°30'S 110°00'E), G1/32/63 (28°55'S 110°00'E).	
International Indian Ocean Exp.		
RV *Anton Bruun* A:	6, 8, 9A, 11.	
1:	30, 33, 51, 53, 57, 58, 60, 67, 70, 78.	
2:	106, 108, 110, 111, 112, 116, 117, 118, 120, 121, 127, 134, 135, 137, 141, 142, 143.	
3:	149.	

TABLE 1.—*Continued*

Location and station		Source of collecting data[1]
4A:	189.	
5:	283, 284, 295, 302, 312, 315, 318, 320, 322, 324, 326A, 327B.	
6:	328, 333.	
7:	370, 371.	
8:	404, 413, 415.	
RV *Argo*		
(Lusiad Exp.):	3, 8, 9, 10, 12, 15, 17, 18, 20, 34, 40, 41, 44, 45, 46, 49, 55, 61, 65, 71, 81, 86, 96.	C
RV *Diamantina*		
2 (1962):	61, 100.	C
1 (1963):	4, 47.	
3 (1963):	113.	
2 (1964):	100A.	
5 (1964):	212.	
1 (1965):	60.	
RV *Discovery* 1:	5031, 5038.	C
RV *Discovery* 3:	5267A, 5269A, 5275, 5371A, 5387, 5400B, 5412A, 5437A, 5548.	
RV *Kagoshima Maru*		
3:	7, 15, 16, 24, 30.	C
RV *Kistna* 13:	296, 301.	C
RV *Koyo Maru*		
14:	19.	C
16:	20.	
RV *Meteor:*	90, 93B, 95B, 114, 116A, 116B, 126A, 130A, 137, 138, 144, 151, 157, 168, 173, 181.	C
RV *Oshoro Maru*		
1:	3, 17, 44, 45, 50.	C
7:	7, 8.	
11:	3, 10, 19, 23.	
RV *Umitaka Maru*		
23:	1-7.	C
24:	6303.	
RV *Varuna* 30:	1775.	C
RV *Vitiaz* 35:	5198A, 5198B, 5200, 5205, 5207, 5208, 5217, 5221, 5224, 5278.	C
36:	5336.	
Lusiad I Exp.:	2, 4.	A
II Exp.:	5, 8, 9, 10, 11, 12, 13, 15, 19, 20, 29, 39, 45, 51, 61, 62, 66, 76, 88, 96.	
V Exp.:	40, 42, 43, 45, 46, 47, 50, 59, 60, 64, 68, 73, 76, 78, 84, 92, 96, 100, 104.	
VI Exp.:	1, 8.	
Monsoon Exp.:	7, 10, 11, 12, 18, 19.	A

PONTELLINA MORII

Pacific Ocean:		
Aries I Exp.:	30 (09°20'S 127°05'W).	
CalCOFI Cruise		
5810:	153.70.	E
Capricorn Exp.:	2, 4, 5, 35.	A
Circe II Exp.:	9, 11, 12, 14.	B
RV *David Starr Jordan*		
57:	116 (07°30'N 119°43.3'W), 123 (07°00'N 120°40'W).	
60:	122 (04°00'N 116°41'W), 134 (07°05'N 116°58'W).	
EASTROPAC Exp.		
RV *Argo* II:	197, 211, 234, 320, 328.	D
RV *Rockaway* 13:	071, 095, 099, 103.	
EQUAPAC Exp.:		
RV *Horizon:*	20, 21, 25, 30, 31, 32, 35.	D
RV *Stranger:*	11, 17, 19.	
RV *Islander VI* (CSIRO):	2/50/70 (15°47'S 137°28'E), 1/9/71 (12°24'S 138°11'E).	
La Pared Exp.:	17F.	B
Monsoon Exp.:	1, 3, 6.	A
Naga Exp. S11A:	83, 127A, 164, 169, 169A.	B
S11B:	5, 10, 16, 17, 20, 24, 27, 31, 36, 41, 46, 66, 78, 86.	
NAVOCEANO RV *Hunt*		
1968 :	14.	B
1969 (May):	9.	
1969 (Oct.):	2, 3.	
1969 (A-14):	7, 9.	
NAVOCEANO RV *Silas Bent:*	1-11, 1-12, 1-16, 1-17, 1-18, 1-20.	B
Piquero V Exp.:	40D, 45D, 48.	B
Scan IV Exp.:	1, 2, 3, 35D, HF 18, DSDP 17, 48D.	B
V Exp.:	4, 5.	
Scorpio II Exp.:	156.	B
Shellback Exp.:	100, 105.	A
TO-58-1 Cruise (Scot):	14.	B
TRANSPAC Exp.:	87B, 92A, 96A, 98B.	A
Troll Exp.:	24A, 25, 25A, 26, 27A, 28, 30, 30A, 31A, 32, 32A.	A
Indian Ocean:		
Circe III Exp.:	22, 23, 25, 26, 27, 29.	B
Dodo VI Exp.:	12, 70, 81, Mombasa Harbor.	A
International Indian Ocean Exp.		
RV *Anton Bruun*		
A:	6, 7, 10A, 11.	C
1:	25, 28, 29, 30, 32, 33, 34, 35, 36, 43, 51, 52, 53, 55, 56, 57, 58, 68, 69, 70, 71, 72, 73, 75, 76, 79.	
2:	106, 108, 109, 110, 111, 112, 113, 114, 120, 121, 123, 142.	
4A:	189, 198.	
5:	283, 284, 323, 287A, 323A, 327B, 327C.	
6:	328, 333, 336	
7:	358, 367, 371.	
8:	413, 414.	
RV *Argo* (Lusiad Exp.):	3, 12, 41, 46, 49, 55, 65, 71, 81, 85.	C
RV *Diamantina*		
2 (1962):	61.	
1 (1963):	47.	C
RV *Discovery*		
1:	5031, 5038.	C
3:	5267, 5269A, 5385, 5412A.	
RV *Kistna:*	296, 298, 301, 304, 514, 515.	C
RV *Meteor:*	90, 91, 93A, 93B, 95B, 96, 106, 114, 116A, 130A, 137, 138, 145, 151, 154, 157, 161B, 168, 186, 198.	C
RV *Natal* 6:	163, 174.	C
RV *Oshoro Maru* 11:	3, 13, 19.	C
RV *Pioneer* 442:	1, 35.	C
RV *Umitaka Maru* 23:	1-7.	C
RV *Varuna* 30:	1775.	C
104:	2007, 2009.	
106:	2041.	
RV *Vitiaz* 35:	5224.	C
Lusiad I Exp.:	2.	A
II Exp.:	1, 10, 11, 13, 14, 16, 27, 55, 62, 66, 90.	
V Exp.:	43, 45, 58, 60, 66, 68, 76, 78.	
VI Exp.:	1, 8.	
Monsoon Exp.:	7, 11, 14.	A

PONTELLINA SOBRINA

Pacific Ocean:		
Bonacca Exp.:	27, 31, 32, 33, 34, 35, 36, 37, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58.	A
CalCOFI Cruise		
5801:	153.50.	E
5804:	Gulf of Panama.	
5807:	Gulf of Panama.	
5901:	157.10.	
6108:	BPT 14.	
Capricorn Exp.:	2, 4, 6, 35.	A

TABLE 1.—*Continued*

Location and station		Source of collecting data[1]
Circe II Exp.:	9, 11, 12, 14.	B
RV *David Starr Jordan*		
57:	002 (13°42'N 120°13'W), 012 (13°16'N 119°23'W), 025 (10°30'N 119°43.5'W), 064 (04°00'N 120°43'W), 076 (03°20'N 119°42'W), 108 (06°32'N 119°50'W), 132 (09°45'N 120°12'W).	
60:	056 (03°22'S 119°30'W), 067 (01°36'N 117°22'W), 071 (02°00'N 117°17'W), 122 (04°00'N 116°41'W), 132 (06°34"N 116°22.3'W), 134 (07°05'N 116°58'W), 148 (09°27.7'N 117°49'W), 156 (10°36'N 117°17'W).	
65:	170 (00°28'N 96°58'W).	
Dragon Exp.:	N-1.	B
EASTROPAC Exp.:		
RV *Argo* 11:	234, 291, 299.	D
RV *David Starr*		
Jordan 12:	033, 037, 041, 059, 063, 077, 100.	
RV *Rockaway* 13:	048, 056, 060, 064, 071, 075, 083.	
El Golfo II Exp.:	XVIII B1-D1, B2-D1, A6-D1, B1-N1.	B
Harpoon Exp.:	13 (16°00'N 95°12'W).	
La Creuse Exp.:	15, 16, 17, 18, 21, OT-1, OT-6, OT-12, OT-14.	B
Muddauber Exp.:	125-4, 126-1, TDS-86.	B
Piquero V Exp.:	40D, 43D, 44.	B
Shellback Exp.:	47, 51, 63, 67, 185.	A
RV *Townsend Cromwell*		
51:	051 (03°15'S 118°23'W), 061 (02°30'S 119°47'W), 064 (03°30'S 120°45'W), 076 (02°28'S 121°42'W), 079 (02°42'N 121°49'W).	
TO-58-1 Cruise (Scot):	16, 17, 27, 29, 31, 32, 33, 35, 36, 37, 38, 42, 45, 46, 48, 56.	B
TO-58-2 Cruise:	9, 16.	B

[1] A Snyder and Fleminger, 1965
B Snyder and Fleminger, 1972
C Anonymous, 1969
D Love, 1972
E Fleminger, 1967a
F Scheltema, 1971 (only chart)
G Anderson, Gehringer, and Cohen, 1956; Anderson and Gehringer, 1958, 1959a, 1959b
H Collier, Drummond and Austin, 1958

area of its geographical distribution. Total length (TL), prosome, i.e., cephalosome and thorax combined (P), and urosome (U) were measured with an ocular micrometer at 50× magnification under a stereoscopic microscope; smaller structures were measured under a compound microscope at 100 × to 400× magnification. The morphological terms and abbreviations in general follow those of Fleminger (1967b).

Measurements, drawings, and descriptions refer to the right side or to appendages from the right side unless stated otherwise. TL and the length of U were measured (Figure 2a) to the distal end of the right furcal ramus, without allowance for any telescoping of segments. The length and width of the furcal rami were measured in dorsal view. In the adult female, the right ramus is fused to the anal segment; the length was obtained from the distance between the medial notch indicating the place of fusion with the anal segment and the insertion of the second innermost furcal seta (Figure 2d). The length of the left furcal ramus was also measured from the medial junction with the anal segment to the insertion of the second innermost furcal seta from the median. In both males and immature females the lengths of the right and left furcal rami were measured from the lateral margin at the proximal end to the insertion of the second innermost seta at the distal end (Figure 2c). For all stages the right furcal ramus was measured across its maximum width (Figure 2c).

The segments of the fifth legs (P5) of the female were measured from the anterior side (Figure 2f). The length of the exopod (Re) was taken as extending from the junction with the second basal segment (B2) to the base of the longest distal seta; the endopod (Ri) was measured from the junction with B2 to the tip of the medial spine. The length of the point on the fifth thoracic segment (ThV) is taken in lateral view as the distance between its tip and its base where the point is delineated by a distinct step or turn to the posterior (Figure 2g). The length of the spermatophore sac was measured as the distance from the distal end to the outer margin of the proximal convolution taking care to position the spermatophore to avoid diminution by an oblique angle of view (Figure 2b). Measurements of segments 13-17 and the succeeding three free segments of the male right antennule (A1) were taken from intact specimens positioned in lateral view (Figure 2e). P5 of the male was measured from the posterior side: the length of the second free segment of the left leg extends from the junction with B2 to the distal margin near the seta (Figure 2h); the length and width of the proximal segment of the chela are, respectively, the shortest distance

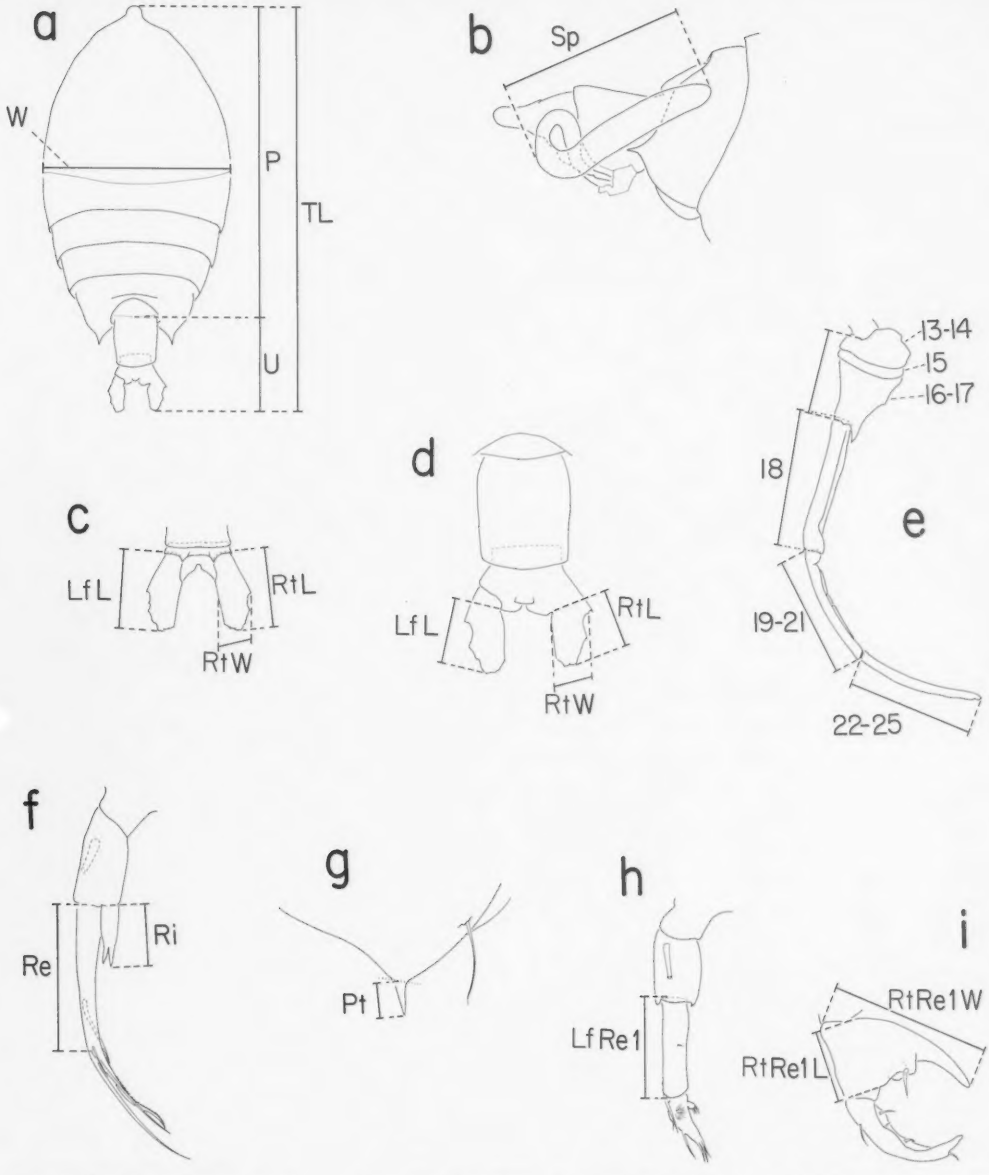

FIGURE 2.—Measurements taken from *Pontellina* specimens. **a**. dorsal view, female; **b**. abdomen with spermatophore, ThIV-V, lateral view, female; **c**. anal segment and furcal rami, dorsal view, male; **d**. urosome, dorsal view, female; **e**. right A1, segments 13-25 male; **f**. right P5, anterior view, female; **g**. spine on right ThIV-V, lateral view, female; **h**. left P5, posterior view, male; **i**. chela of right P5, posterior view, male. L = length; Lf = left; P = prosome length; Pt = spine; Re = exopod; Re1 = first exopodal segment; Ri = endopod; Rt = right; Sp = spermatophore; TL = total length; U = urosome length; W = prosome width.

between the shallow swelling in the proximal lateral corner and the distal margin, and the distance between the proximal medial corner and the tip of the large lateral prong (Figure 2i).

Types and reference specimens have been deposited with the Smithsonian Institution, U.S. National Museum, Washington, D.C.

GENUS *PONTELLINA* DANA

Pontella Dana, 1846 (in part), p. 184, type not designated; Dana, 1849, p. 26, type not designated.

Pontellina Dana, 1853 (in part), p. 1135, type not designated; Giesbrecht, 1889, p. 29, type by monotypy, *Pontellina plumata* (Dana); Giesbrecht, 1892, p. 73, 497; Giesbrecht and Schmeil, 1898, p. 149.

Calanops Claus, 1863, p. 211, type by monotypy, *Calanops messinensis* Claus = *Pontellina plumata* (Dana), Giesbrecht, 1889, p. 29.

Pseudopontia Claus, 1892, p. 861, 864, type by monotypy, *Pseudopontia plumata* (Dana) = *Pseudopontella plumata* (Dana), Claus, 1893, p. 278.

Pseudopontella Claus, 1893, p. 278, type by monotypy, *Pseudopontella plumata* (Dana) = *Pontellina plumata* (Dana), Giesbrecht and Schmeil, 1898, p. 149.

Not *Pontellina* Claus, 1892, p. 851; 1893, p. 272.

Diagnosis

Relatively small pontellids, less than 2 mm in TL. Prosome in dorsal view broadly oval, less than twice as long as maximum width; forehead lacking headhooks; ThIV-V corners symmetrical; rostrum proximally protuberant, bifurcate at base, and extending ventrad as slender, elongate, flexible filaments; in lateral view, filaments more than 10 times longer than wide at maximum width; ventral eye present but inconspicuous, scarcely produced, and lacking a distinctive lens. In A1 (except sexually modified right A1 of male) segments 13, 14, and 15 separate and about equal in length. A2 with Re about as long as Ri1, length of Ri1 less than 4 times maximum width.

Female lacking distinctive dorsal lenses in forehead. Furcal rami weakly asymmetrical, right ramus fused to anal segment. P5 with monomerous Re bearing 1 lateral and 3 terminal setae, in addition to one medial setiform process fused to Re and serrated along medial margin; Ri monomerous and terminating in one or two apical spines. A2 and mandible (Mnd) with elongate setae reaching beyond thorax when extended posteriad.

Male with one pair of dorsal lenses in forehead.

Additional Description

Both sexes with cephalic groove and agreeing in meristic features of all appendages except for those modified by sexual maturation. Nonsexually modified appendages agree with those of *Pontellina plumata* as shown by Giesbrecht (1892, pl. 25, fig. 1, 6, 7, 9, 12-14, 18, 20, 21, 23-25). Segmentation, setation, and spination of nonsexually influenced appendages are virtually identical among the four species and, except for A1, closely resemble those of *Pontellopsis*. They are as follows:

A1: 17 free segments; segments 2-5, 6-8, 24-25 fused, 9-11 partly fused.

A2: 2 basal segments; Re: 3 segments with 1, 4, 3 setae, respectively; Ri: 2 segments; Le: 6, Li: 6 + 2 setae.

Mnd: palpus 1 seta; Re: 5 segments with a total of 6 setae; Ri: 2 segments with 4 and 6 setae, respectively.

Mx1: Li1: 14 spines; Li2: 3 spinelike setae; Li3: small, 3 setae; B2: 3 + 2 setae; Ri: 4 + 1 setae; Re: 8 setae; Le: 1 + 8 setae.

Mx2: lobe 1: 3 + 1 setae; lobes 2-5: 2 + 1 setae each; Ri: 6 + 1 setae.

Mxp: 5-segmented, fingered lobe on B1 with 2, 2, 3 setae.

P1: trimerous Re: 1, 1, 4 Si; 1 St; 1, 1, 2 Se; trimerous Ri: 1, 2, 4 Se; 1 St; 0, 0, 1 Se.

P2 and P3: trimerous Re: 1, 1, 5 Si; 1 St; 1, 1, 3 Se; bimerous Ri: 3, 5, Si; 1 St; 0, 2 Se.

P4: trimerous Re: 1, 1, 5 Si; 1 St; 1, 1, 3 Se; bimerous Ri: 3, 4 Si; 1 St; 0, 2 Se.

Se of P1 smooth; Se of Re1 and Re2 of P2 with toothed medial margin; Se of Re3 with toothed medial and lateral margins; in Se of P3 and P4 also both margins toothed.

St of Re 3 of P1 to 4 with toothed lateral margin.

B1 of P1 to 4 with 1 Si; B2 ususally without setae.

Right A1 in male with segments 13-17 swollen, 13-14 and 16-17 fused; length of swollen section varies considerably due to either telescoping of segments or expansion of articulations. Distal three free segments slender and consisting of segment 18 followed by a compound segment formed by fusion of segments 19-21, and ending in a compound segment fusing segments 22-25.

Mandibular blade (Giesbrecht 1892, pl. 25, fig. 14) bearing a one-pointed apical (ventral) tooth, a two-pointed subapical tooth, two deeply cut two-pointed medial teeth, and three basal (dorsal) teeth; basal seta lacking; dorsal accessory bristles exceed teeth in length; patches of spinules appear on anterior side of blade.

P5 segmentation in both sexes typically pontellid; B2 of male bearing a large plumose seta on posterior surface, Ri lacking, Re bimerous; right leg with elongate B1, cheliform Re; left leg with reduced B1 fused to precoxa, distal segment of Re armed with four short setiform processes.

Spermatophore with relatively long neck bearing one full counterclockwise turn relative to proximal end, helix occurring between spermatophore sac and place of attachment located in a cement mass overlying genital pore of female. Elongate spermatophore neck may also be connected secondarily to right side of genital segment proximal to helix, thereby orienting sac dorsad or anterodorsad with helix and sac flanking right side of genital segment. When secondary lateral cementation absent, neck, helix, and sac hang free from ventral side of genital segment.

PONTELLINA PLUMATA (DANA)

(Figures 3 and 4)

Pontella plumata Dana, 1849, p. 27 (type locality not designated); Brady (in part), 1883, p. 92, pl. 37, fig. 1-10 only.

Pontella turgida Dana, 1849, p. 28 (type locality not designated).

Pontellina plumata: Dana, 1853, p. 1135; Dana, 1855, pl. 79, fig. 10; Giesbrecht, 1889, p. 29; Giesbrecht, 1892, p. 497, pl. 4, fig. 1, pl. 25, fig. 1, 4, 6, 7, 9, 12-14, 18, 20, 21, 23-26, 36, pl. 40, fig. 49-53; Mori (in part), 1937, p. 99, pl. 47, fig. 7-11 only; Grice, 1962, p. 240, pl. 34, fig. 11-15; Brodsky, 1962, p. 147, fig. 47; Park, 1968, p. 569, pl. 13, fig. 15-16.

Pontellina turgida: Dana, 1853, p. 1136; Dana, 1855, pl. 79, fig. 11, 12.

Calanops messinensis Claus, 1863, p. 212, pl. 2, fig. 11, pl. 36, fig. 13-16, pl. 37, fig. 10 (Messina).

Pontellopsis speciosus Brady, 1915, p. 138, pl. 10, fig. 1-8 (Durban Bay). NEW SYNONYMY.

Pontellopsis aequalis Mori, 1932, p. 172, 175, pl. 4, fig. 7-13 (25°20′50″N, 124°7′30″E).

not *Pontella plumata:* Brady (in part), 1883, p. 93, pl. 37, fig. 11 only.

not *Pontellina navalium* Oliveira, 1947, p. 472, fig. 12; Vervoort, 1965, p. 191.

Specimens seen: 1,259 adult females, 917 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.69	1.44-1.94	0.0126	75
Male	1.51	1.34-1.92	0.0130	67

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.28:1	2.92-3.72:1	75
Male	3.07:1	2.84-3.93:1	52

Diagnosis

Female

Posterior corner of ThIV-V in lateral view produced into conspicuous spiniform process of characteristic shape (Figure 3 a, b, d-g). Ventral margin of spine more or less continuous with ventral margin of ThIV-V, transition with dorsal margin abrupt and stepped; junction of distal end of spine and thicker basal portion usually set off by weak shoulder, spine extending posteriad, sometimes tilted weakly ventrad or dorsad. In dorsal view spine more or less continuous with posterior tapering of corner, shoulder or constriction sometimes present; spine usually directed posteriad and slightly laterad, sometimes straight or turned slightly mediad.

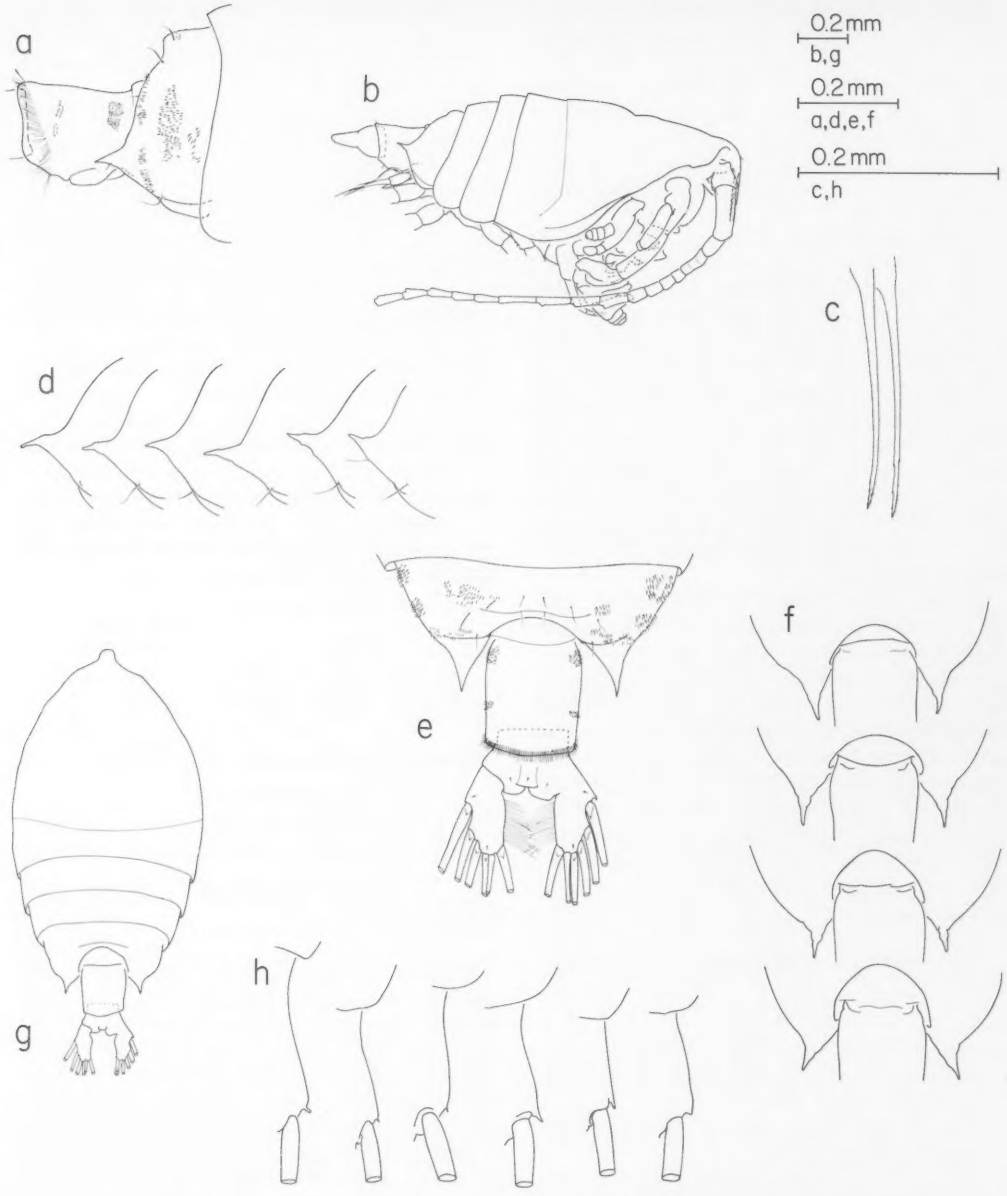

FIGURE 3.—*Pontellina plumata* s.str., adult female: **a**. ThIV-V, genital segment, lateral view (TRANSPAC 96A); **b**. habitus, lateral view, swimming legs incomplete (same station as **a**, different specimen); **c**. rostral filaments, lateral view (*Atlantis II*-31-2); **d**. range of variation observed in ThIV-V, lateral view (left to right: Lusiad VI-8; *Chain* 49-11; Lusiad II-66; *Chain* 49-11, different specimen; *Atlantis II*-31-73; same station, different specimen); **e**. ThIV-V, urosome, dorsal view (same specimen as **a**); **f**. range of variation observed in ThIV-V, dorsal view (top to bottom: Scorpio II-118; *Chain* 49-11; same station, different animal; *Chain* 49-20); **g**. habitus, dorsal view (same specimen as **b**); **h**. lateral margin of right furcal ramus of various specimens, dorsal view (left to right: *Atlantis II*-31-2; Troll 28A; *Atlantis II*-20-22; Dodo VI-65; Troll 25; Scorpio II-182).

Genital segment bearing anterolateral and posterolateral clusters of hairs on both sides of segment (Figure 3 a, e); anterior cluster larger, best seen in dorsal view. Posterior cluster less prominent, of similar or coarser hairs. A row of relatively long, fine hairs encircling segment near distal margin.

Male

In lateral view posterior corner of ThIV-V somewhat angular, apex usually bearing one minute denticle (Figure 4e-h). Chela of right P5 with proximal segment extending distolaterad as a relatively slender digitiform process opposing apex of distal falcate segment (Figure 4i); base of distolateral digitiform process flanked by small anterior process, triangular in lateral view, and small angular posterior process bearing a sensoriiform seta (Figure 4j); in lateral view posterior basal process and digitiform process with relatively straight margins intersecting at an angle greater than 70° (Figure 4j); in posterior view two basal processes overlapping, both extending toward center of lumen of chela; additional sensoriiform setae on proximal segment of chela: one anteromedial near articulation with distal segment; on distal segment: one proximomedial, one mediosubapical, and three lateral. Left P5 (Figure 4i) with proximal segment of Re (Re1) short relative to other three species below. Length of right furcal ramus exceeds left Re1 by 1.55-1.85 times, 46 specimens (see Figure 30).

Additional Description

Female

Right furcal ramus fused to anal segment, varying directly with prosome length, relatively longer than that in Indian and Pacific congeners described below (Figure 25); ratio of length to width highest in genus, usually 1.5 times longer than wide (median 1.56:1, range 1.28-1.74:1, 134 specimens), showing apparent overlap only with the equatorial Atlantic congener (see Figure 27); lateral margin of right furcal ramus with small pointed projection somewhat variable in shape and size just anterior to base of outermost seta (Figure 3e, h). Glandlike tissue within right furcal ramus with associated ductlike structure extending toward lateral point. Left furcal ramus not fused and appreciably longer than right ramus (see Figure 19).

P5 (Figure 4a, c, d) with inner margin of Re lacking hair, Ri polymorphic with one or two apical spines fused to segment, spines on left and right Ri may differ in number in same specimen (Figure 4b, Table 7); Re 2 to 3 times longer than Ri, median 2.37:1, range 1.97-3.08:1, 59 specimens, differing strongly from Indian and Pacific congeners (see Figure 29).

Attached spermatophore observed on four specimens (see Figure 33 a, b; Table 5), hanging free from single place of attachment in vicinity of genital pore, neck with small helical turn near place of attachment and larger helical turn at origin of sac.

Male

Right furcal ramus not fused to anal segment, about equal in length to left ramus (see Figure 19), varying directly with prosome length (see Figure 26); ratio of length to width relatively high (median 2.30:1, range 2.0-2.53:1, 44 specimens), but showing more overlap with congeners than found among females (see Figure 28).

Types

Unknown, presumed to be lost. Reference specimens from the Atlantic, Pacific, and Indian Oceans have been deposited in the U.S. National Museum, Smithsonian Institution.

Reference Specimens

4 ♂, 4 ♀, *Atlantis II*-31-5, lat. 39°13.0′N, long. 63°26.5′W, 14 Jan. 1967, ¾-m net, oblique tow, maximum cable out 200 m.

2 ♂, 2 ♀, Capricorn 31, lat. 06°31′N, long. 124°41′W, 13 Feb. 1953, 1-m net, oblique tow, maximum cable out 200 m.

2 ♂, 2 ♀, TRANSPAC 134A, lat. 23°26.3′N, long. 161°49.6′W, 17 Nov. 1953, 1-m net, oblique tow between surface and 129 m est.

2 ♂, 4 ♀, Lusiad V-76, lat. 02°01′S, long. 91°58′E, 24 Apr. 1963, 1-m net, oblique tow, maximum cable out 280 m.

2 ♂ Lusiad V-104, lat. 03°01′S, long. 52°58′E, 10 May 1963, 1-m net, oblique tow, maximum cable out 280 m.

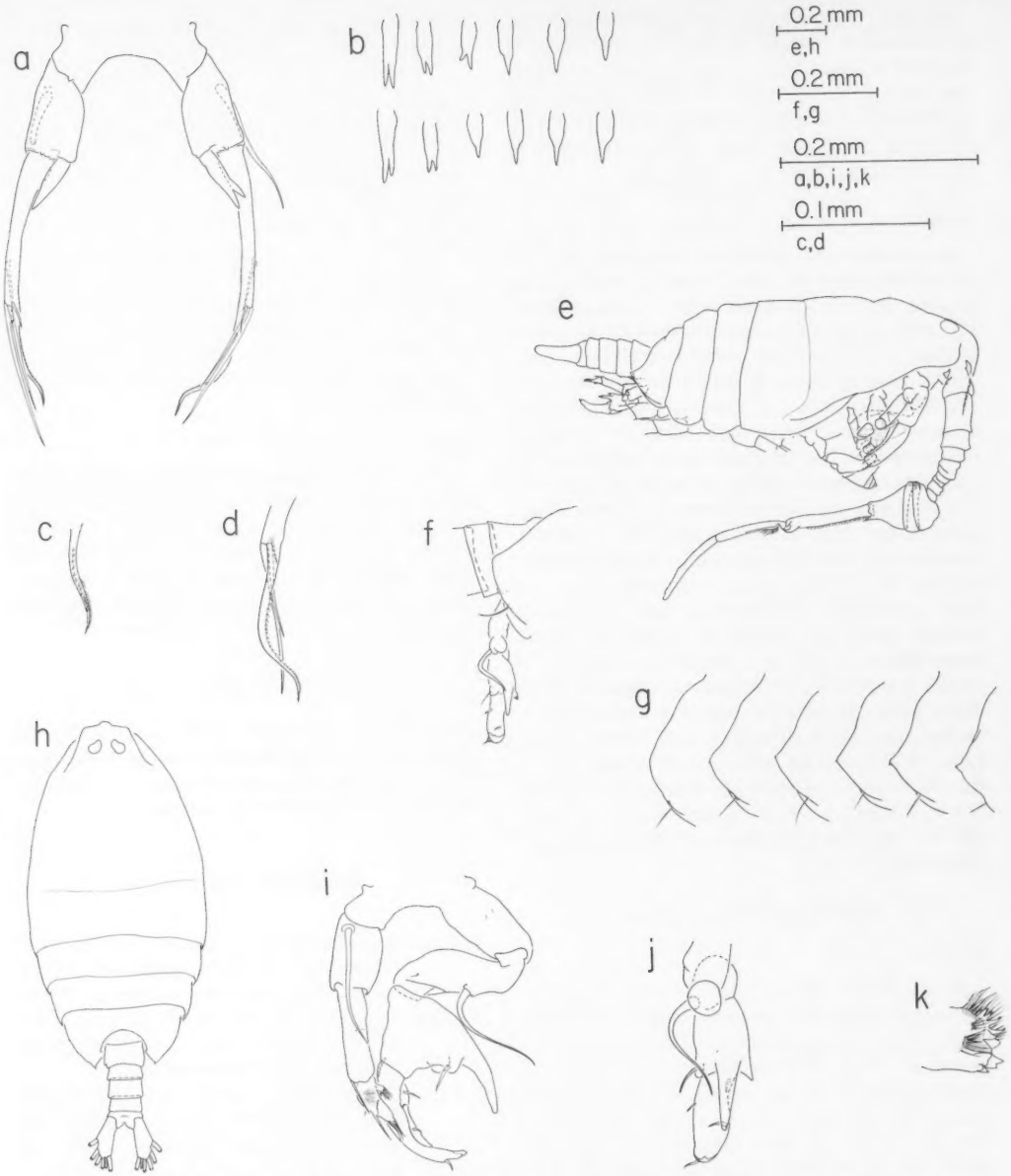

FIGURE 4.—*Pontellina plumata*, s.str. Adult female: **a.** P5 anterior view (TRANSPAC 96A); **b.** P5 Ri of other specimens, right side above, left side below (left to right: Scorpio II-146; Lusiad II-66; La Creuse 3; same station, different specimen; *Atlantis II*-31-6; Lusiad V-45); **c.** enlargement of P5 apex; **d.** enlargement of P5 Re distal process (TRANSPAC 96A). Adult male: **e.** habitus, lateral view (*Atlantis II*-31-28); **f.** ThIV-V, part of urosome, P5, lateral view (TRANSPAC 92B); **g.** variation observed in ThIV-V, lateral view (left to right: Dodo VI-70; *Gill* 8-9; La Creuse 7; *Gascoyne* G1/5/63; Circe NT-38; Monsoon 18). **h.** habitus, dorsal view (same as **e**); **i.** P5, posterior view (same as **f**); **j.** P5 chela, lateral view (same as **f**); **k.** mandible, gnathobase, lateral view.

Remarks on Synonymy and Variability

Dana (1849, 1853, 1855) described the male and female of *P. plumata* as separate species based on specimens obtained from several equatorial localities (in the Atlantic Ocean: lat. 08°30′N to 00°, long. 23° to 18°W; 00°15′N, 31°00′W; 01°00′ to 04°30′S, 17°30′ to 21°30′W; 04°30′S, 25°00′W). Our efforts to use his descriptions and illustrations to separate the two species in our Atlantic collections were fruitless. Moreover, Dana's specimens of *Pontellina* are apparently lost (T. E. Bowman, in litt.).

The present concept of *P. plumata* originates from Giesbrecht's (1892) redescription and synonymy which have been generally accepted. Hence we regard his description of the species as the basis for the type species of the genus.

Several authors have noted morphological variation in *plumata*, observations that may indicate that they had examined specimens of two or more of the four species we recognize in the genus. Thus, Dana (1853) reported that the furcal rami were relatively longer in males from the Cape of Good Hope region than in males from the Pacific Ocean. Giesbrecht (1892) found that the posterolateral corners of ThIV-V were longer in males from the Pacific than in those from waters off Naples. Tanaka (1964) mentions differences in the posterolateral corners of ThIV-V in both sexes of *plumata*. Mori (1937) believed the differences he encountered in specimens of *Pontellina* were a function of ontogeny. On the other hand, a number of authors have published illustrations which appear to be based solely on *plumata* specimens (e.g., Giesbrecht, 1892; Brodsky, 1962; Grice, 1962; Park, 1968).

Distribution

P. plumata exhibits a warm-water circumglobal distribution bounded in the north and south roughly by the subtropical convergence zones of each hemisphere (Figure 5). Adults were frequent in occurrence but relatively low in abundance. For example, in 131 zooplankton samples containing the species from the Indian and Pacific Oceans (Indian Ocean Standard Net and CalCOFI Standard Net zooplankton samples; tows through the epipelagic layer) abundance estimates ranged from 0.002 to 0.4 adults per m^3 water strained, the median being 0.02. In the sets of samples selected for quantitative analysis (Figure 1b) the species appeared infrequently and in minimal numbers in the eastern tropical Pacific. In the remainder of the equatorial Pacific and in the Indian Ocean *plumata* was found in about half of the samples examined.

Values of mean abundance in temporally and geographically related sets of samples usually exceeded 0.02 per m^3 of water strained (see Figure 35, Table 14). With regard to the Atlantic Ocean our impressions from the available nonquantitative collections is that the abundance of *plumata* is not appreciably different from that in the Indian and Pacific Oceans.

The widespread co-occurrence of three sibling species (described below) imposes serious reservations on the use of previously published records of *plumata*. It would be best to consider earlier records primarily as evidence of the occurrence of the genus, a useful attribute considering the virtual absence of the genus at latitudes above 40°.

PONTELLINA PLATYCHELA SP.N.

(Figures 6 and 7)

Specimens seen: 168 adult females, 466 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.70	1.54-1.96	0.0173	30
Male	1.56	1.41-1.74	0.0089	57

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.44:1	3.19-3.89:1	30
Male	3.22:1	2.86-3.55:1	49

Diagnosis

Female

Posterolateral corner of ThIV-V ending in a relatively minute dentiform process extending posteriad or weakly medioposteriad (Figure

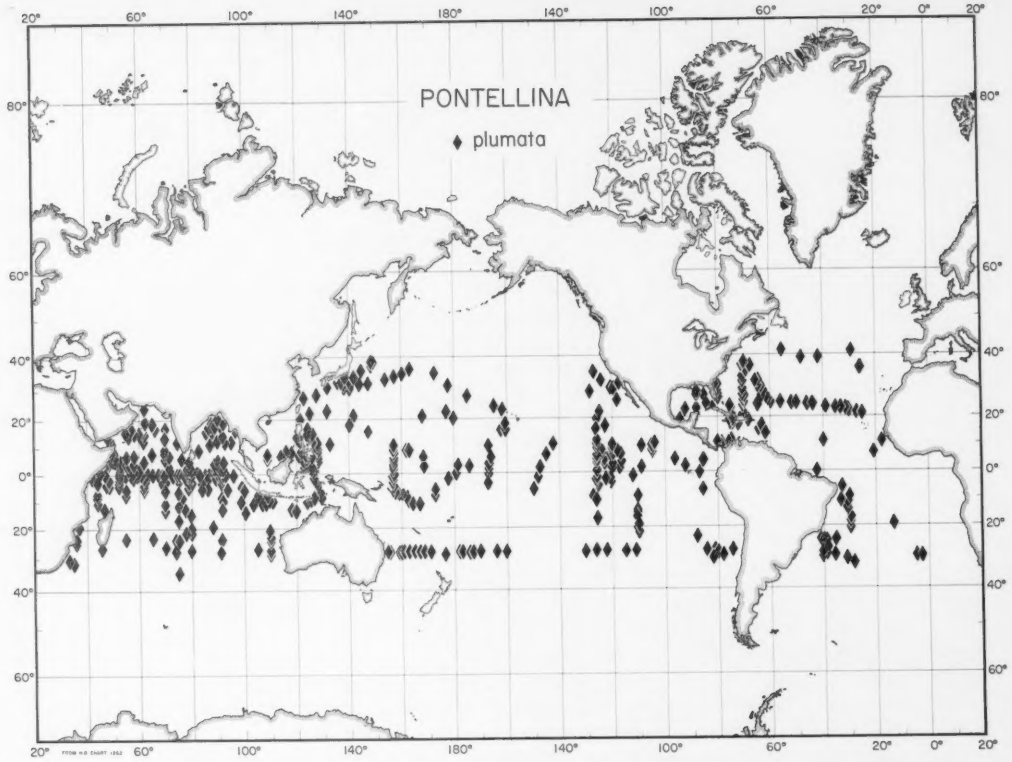

FIGURE 5.—*Pontellina plumata* s.str. Geographical distribution of captures recorded during the present study.

6a-c, f-h); in dorsal view denticle not sharply set off from tapering lateral margin of ThIV-V. Genital segment (Figure 6f, g) with several isolated lateral sensory hairs and line of slender hairs along distal margin, lacking lateral clusters of coarse hairs.

Male

Posterolateral corners of ThIV-V in lateral view tending to be rounded and lacking denticle (Figure 7c, d). Chela of P5 differing markedly from that in *plumata* due to strong anteroposterior expansion of both segments (Figure 7a, b); distal segment spatulate; in proximal segment base of laterodistal digitiform process greatly expanded; in posterior view posterior basal process barely differentiated but sensoriform seta present, anterior basal process relatively small, and extending toward center of lumen of chela. Left P5 (Figure 7a) with proximal segment of Re (Re1) somewhat longer than that in *plumata*, length of right furcal ramus exceeds Re1 by 1.3-1.5 times, 21 specimens (see Figure 30).

Etymology

The name *platychela* is derived from the Greek words platys (= broad) and chela (= crab's claw) and refers to the relatively large chela of the adult male.

Types

Holotype: Adult male, TL 1.52 mm, PUR 3.22:1; sorted from plankton sample taken at *Atlantis II*-31 stn. 48, lat. 00°56′N, long. 25°20′W, 12 Feb. 1967, ¾-m net, oblique tow, maximum cable out 200 m. USNM No. 141613.

Allotype: Adult female, TL 1.72 mm, PUR

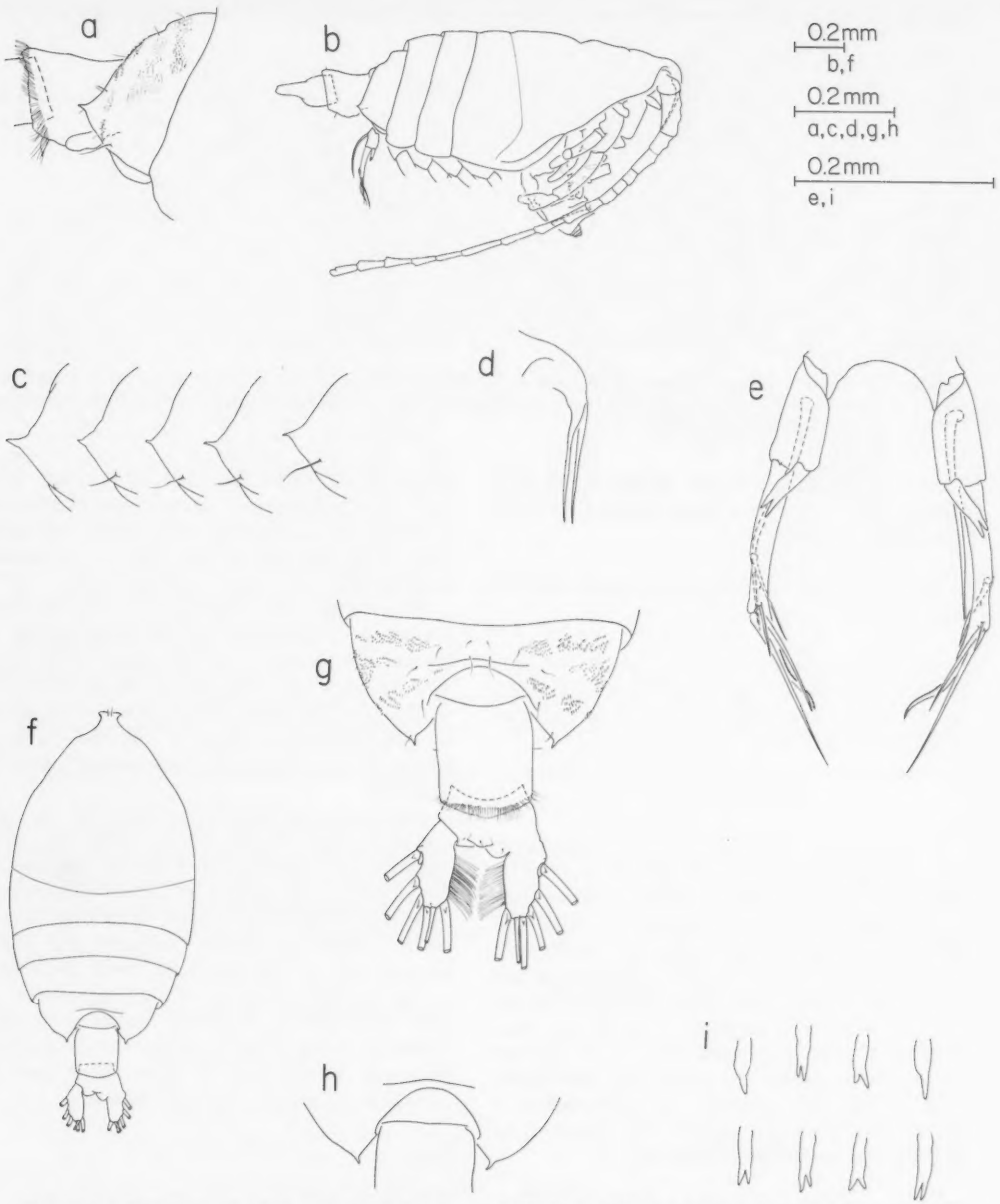

FIGURE 6.—*Pontellina platychela*, sp.n., adult female: **a.** ThIV-V, genital segment, lateral view (*Atlantis II*-20-28); **b.** habitus, lateral view (*Atlantis II*-20-2); **c.** range of variation in ThIV-V, lateral view (left to right: Lusiad VII-81 H13; *Atlantis II*-31-40; Lusiad VII-81 H13, different specimen; *Atlantis II*-20-31; same station, different specimen); **d.** rostrum, lateral view (same as **a**); **e.** P5, anterior view (same as **a**); **f.** habitus, dorsal view (same as **b**); **g.** ThIV-V, urosome, dorsal view (same as **a**); **h.** ThIV-V, dorsal view, another specimen (*Atlantis II*-20-31); **i.** P5 Ri of other specimens, right side above, left side below (all four specimens Lusiad VII-69 H4).

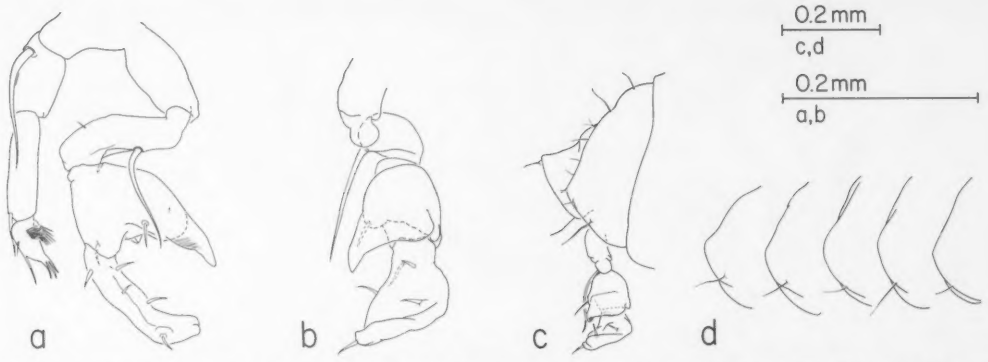

FIGURE 7.—*Pontellina platychela* sp.n., adult male: **a.** P5, posterior view (*Atlantis II*-20-24); **b.** P5 chela, lateral view (same as **a**); **c.** ThIV-V and P5, lateral view (*Atlantis* II-20-27); **d.** range of variation in ThIV-V (left to right: 3 specimens Amazon 17; La Creuse 7; *Oregon* 1293).

3.52:1; right furcal ramus length 0.110 mm, width 0.075 mm; from same sample as male. USNM No. 141614.

Paratypes: 3♂, 3♀ from same sample. USNM No. 141615.

Reference specimens: 5♂, 5♀, *Oregon* stn. 1293, lat. 19°55′N, long. 74°10′W, 23 Apr. 1955, G III net towed between surface and 2m. USNM No. 141616.

Distribution

P. platychela was found only in epipelagic tows taken in equatorial latitudes of the Atlantic Ocean (Figure 8). The species appeared regularly in samples collected between lat. 10°S and 10°N. The more extensive sampling available to us from north of the equator indicates that few *platychela* extend as far as lat. 21° or 22°N and that the species disappears abruptly at higher latitudes. We anticipate that in the vicinity of the Gulf Stream its northward occurrence may be extended somewhat by examination of additional samples, paralleling occurrences to the south in the Brazil Current.

Additional Description

Female

Right furcal ramus somewhat shorter than in *plumata* (see Figure 27), typically 1.4 times longer than wide (median 1.44:1, range 1.28-1.55:1, 35 specimens), lateral process anterior to proximal seta lacking, but interior of ramus with glandlike tissue and ductlike structure leading to lateral margin as in *plumata*.

P5 (Figure 6e) essentially as in *plumata* including proportional length relationship of Re and Ri, median 2.27:1, range 1.69-2.91:1, 49 specimens (see Figure 29); Ri polymorphic with one or two apical spines fused to segment, in same specimen spines on left and right Ri may differ in number as in *plumata* (Figure 6i, Table 7).

Attached spermatophore observed in one specimen (see Figure 33c-e, Table 5); neck cemented to ventral side of genital segment in vicinity of genital pore and buried within large irregular mound of cement extending across entire length of genital segment and right ventral side of anal segment, neck extending to right anterolateral side of anal segment along with continuation of cement fixing it to anal segment, large helical counterclockwise turn following emergence of neck from cement orienting succeeding sac anterodorsad.

Male

Right furcal ramus as in *plumata* (see Figures 19, 26), but relatively wider (see Figure 28), ratio of length to width typically 2:1 (median 2.06:1, range 1.91-2.34:1, 37 specimens).

Our impression from the available Atlantic

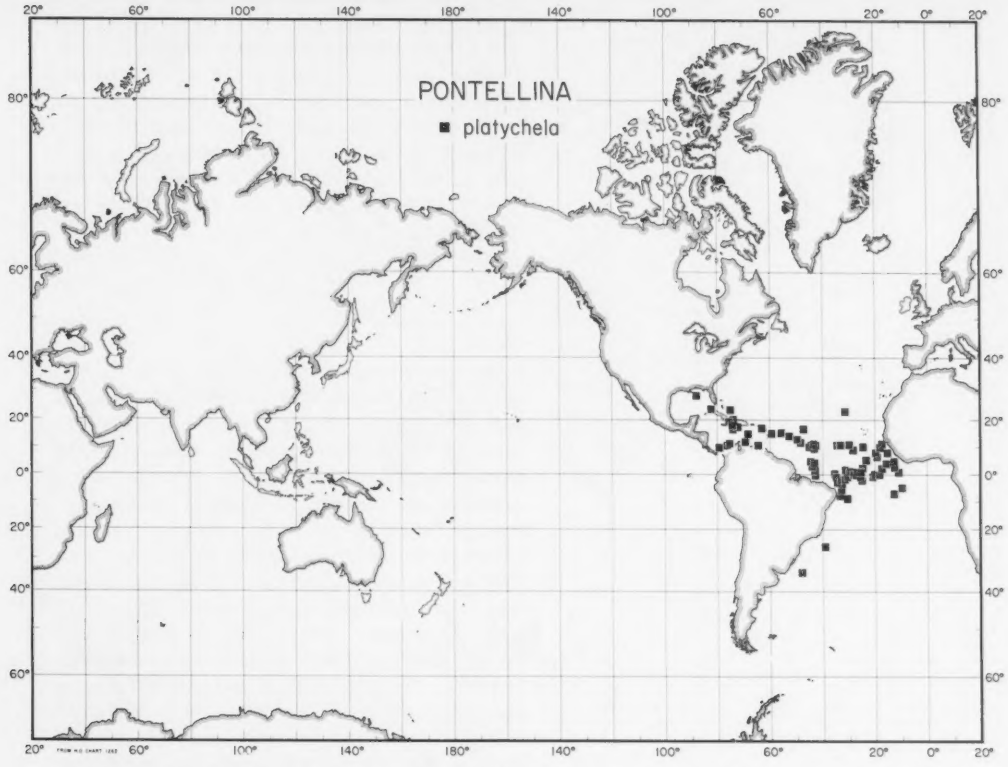

FIGURE 8.— *Pontellina platychela* sp.n. Geographical distribution of captures recorded during the present study.

collections is that the abundance of *platychela* is generally similar to the numbers of *Pontellina* in the Indian and Pacific Oceans (cf. Tables 14, 18), i.e., typically less than 0.2 adults per m^3 of water strained.

PONTELLINA MORII SP.N.

(Figures 9 and 11)

Pontellina plumata: Mori (in part), 1937, p. 99, pl. 48, fig. 1-12 only; Dakin and Colefax, 1940, p. 99, fig. 139. NEW SYNONYMY.

Specimens seen: 433 adult females, 284 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.61	1.38-1.88	0.0145	54
Male	1.44	1.26-1.68	0.0100	58

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.64:1	3.39-4.10:1	35
Male	3.34:1	2.87-3.73:1	50

Diagnosis

Female

Posterolateral corner of ThIV-V ending in a short spiniform process extending posteriad or somewhat medioposteriad; in contrast to *plumata* junction of spine and ThIV-V corner relatively

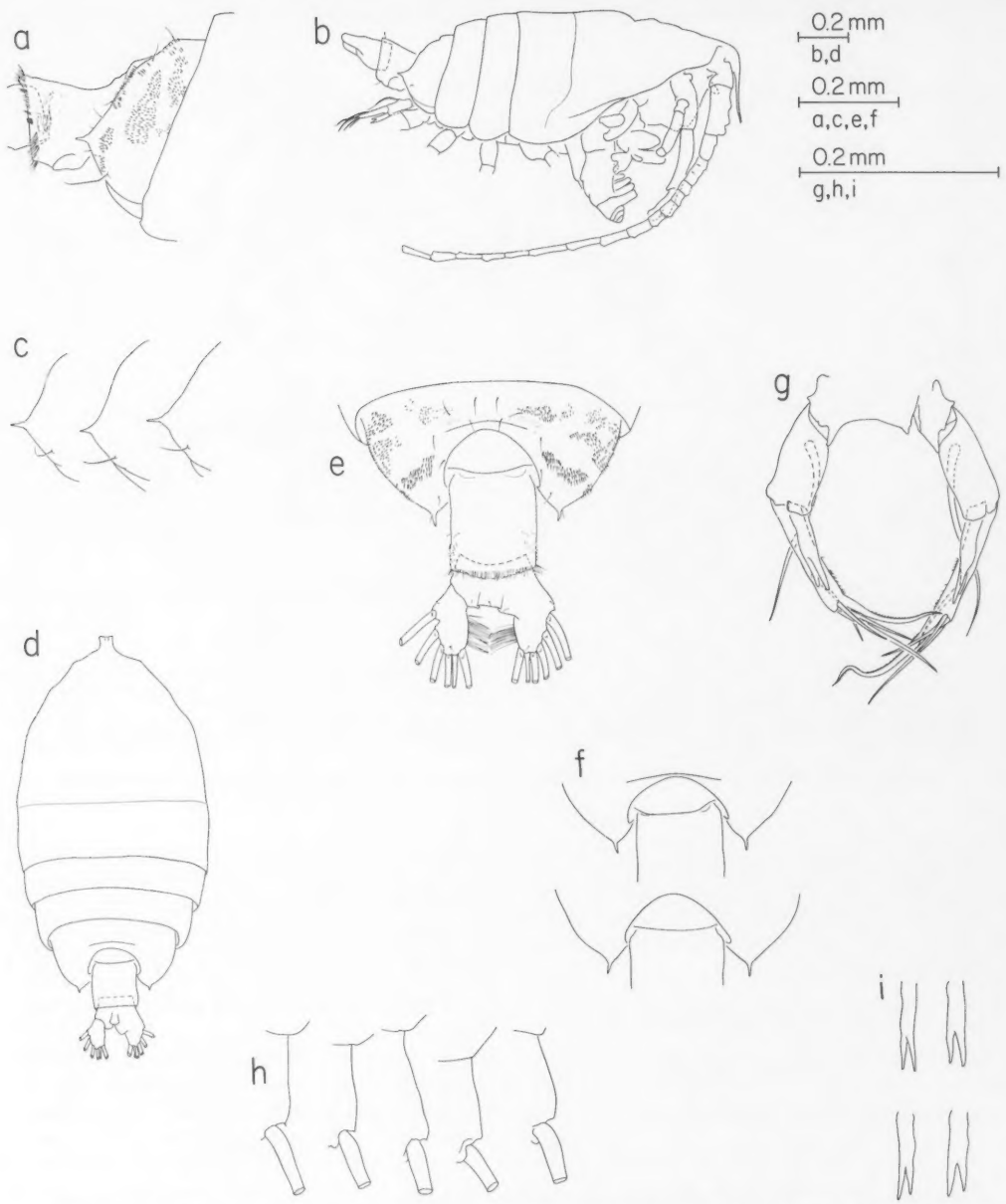

FIGURE 9.—*Pontellina morii* sp.n., adult female: **a.** ThIV-V and genital segment, lateral view (Lusiad V-66); **b.** habitus, lateral view (Circe III NT-27); **c.** variation in ThIV-V, lateral view (left to right: Troll 31A, 2 specimens Lusiad II-66); **d.** habitus, dorsal view (Circe III NT-26); **e.** ThIV-V and urosome, dorsal view (same as **a**); **f.** variation in ThIV-V, dorsal view (top: Troll 31A; bottom: Lusiad II-66); **g.** P5, anterior view (Lusiad V-66); **h.** variation observed in lateral margin of right furcal ramus, dorsal view [left to right: Scan IV-3; TO-58-1 (Scot) 14; Lusiad II-13; Lusiad II-10; Lusiad V-45]; **i.** P5 Ri in other specimens, right side above, left side below (left: Troll 30; right: Silas Bent 1-12).

abrupt in both dorsal and lateral views (Figure 9a-f), right and left sides symmetrical (Table 2), spine small, not exceeding 0.035 mm irrespective of TL (Figure 10), spine roughly one-half as long as that in its congener from the eastern equatorial Pacific described below. Genital segment with posterolateral cluster of coarse hairs on both sides, lacking anterolateral cluster found in *plumata* although several fine hairs may occur at this site (Figure 9a, e): posterior margin of segment bordered by fine, long hairs as in *plumata*.

Male

ThIV-V typically ending posteriorly in a small spiniform process (Figure 11b, c) similar to female. P5 with chela of *plumata*-type but both segments showing distinctive features; distal segment short, not reaching opposing disto-lateral digitiform process on proximal segment (Figure 11d), apex of distal segment with prominent triangular spur on posterior side (Figure 11d-f); proximal segment in lateral view with basal process posterior to digitiform process acuminate, intersection of posterior basal process and digitiform process usually in form of a deep angular notch; in posterior view proximal segment with axis of posterior basal process extending somewhat parallel to digitiform process and not overlapping anterior basal process, latter angled toward articulation between proximal and distal segments. Left P5 with Re1 longer than that in *plumata* (see Figure 30).

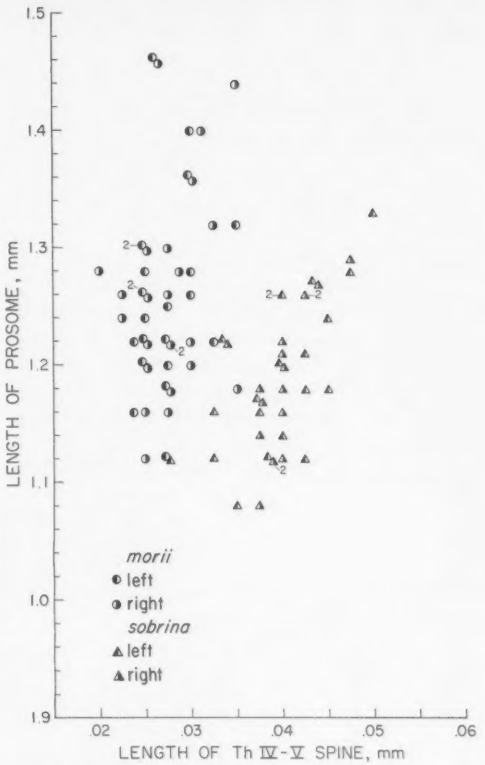

FIGURE 10.—Length of prosome (ordinate) plotted against length of ThIV-V spine (abscissa) for females of *Pontellina morii* and *P. sobrina*.

Additional Description

Female

Right furcal ramus considerably shorter than in *plumata* relative to prosome (see Figure 25), right furcal ramus with median ratio of length to width 1.25:1, range 1.12-1.44:1, 46 specimens; lateral edge of right ramus with small point variable in shape just anterior to base of outermost seta (Figure 9e, h), glandular tissue within ramus as in *plumata*.

P5 with Re bearing hairs along median margin (Figure 9g); Ri relatively longer than that

TABLE 2.—Length of posterior spine on thoracic segment IV-V in adult females of *Pontellina morii* and *P. sobrina*.

Species		$\bar{x}$ (mm)	Range (mm)	s	N
P. morii	left side	0.0263	0.018-0.035	0.0010	38
	right side	0.0275	0.020-0.035	0.0032	40
	combined	0.0269	0.018-0.035	0.0037	78
P. sobrina	left side	0.0409	0.033-0.050	0.0032	33
	right side	0.0404	0.028-0.049	0.0032	32
	combined	0.0407	0.028-0.050	0.0045	65

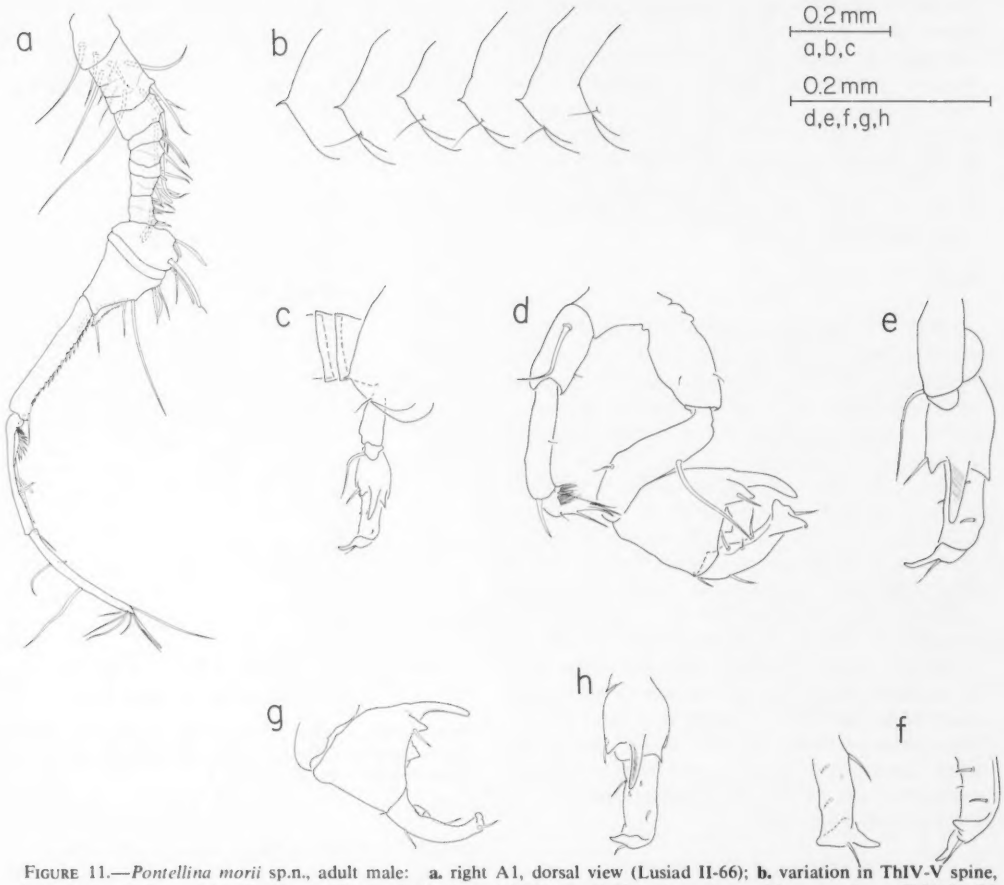

FIGURE 11.—*Pontellina morii* sp.n., adult male: **a.** right A1, dorsal view (Lusiad II-66); **b.** variation in ThIV-V spine, lateral view (left to right: Shellback 105; Troll 25; Lusiad II-55; Troll 32A; 2 specimens Monsoon 6); **c.** ThIV-V, P5 and first two segments of urosome, lateral view (Lusiad V-78); **d.** P5, posterior view (same as **a**); **e.** P5 chela, lateral view (same as **c**); **f.** apex of distal segment of P5 enlarged (same as **c**); **g.** aberrant chela showing a weakened subapical spur on distal segment, posterior view (*Anton Brunn I*-58); **h.** aberrant chela, lateral view (same as **g**).

in *plumata*, Re being less than 1.8 times longer than Ri, median 1.45:1, range 1.22-1.76:1, 55 specimens (see Figure 29); Ri typically with two relatively equal apical spines (Figure 9g, i; Table 7).

Attached spermatophore observed in four specimens (see Figure 33f-h, Table 5), appearance and orientation similar to that in *platychela* except for less cement on ventral side of urosome, especially on anal segment.

Male

Right furcal ramus differing from that in *plumata* in having a relatively shorter length (see Figure 26), median length-to-width ratio 1.93:1, range 1.80-2.07:1, 39 specimens, but overlapping extensively with its congener from the eastern equatorial Pacific (described below). Left P5 with Re1 considerably longer than that in *plumata:* in *morii* length of left P5 Re1 to length of right furcal ramus ranges from 1.08 to 1.26:1, 20 specimens (see Figure 30).

Etymology

This patronym commemorates the late

Takamochi Mori who first called attention to the distinctiveness of this species and for his pioneering contributions to our knowledge of Pacific Calanoida.

Types

Holotype: Adult male, TL 1.36 mm, PUR 3.25:1; sorted from plankton sample taken at Lusiad II stn. 66, lat. 01°54′N, long. 79°01′E, 30 Aug. 1962, 1-m net, oblique tow, maximum cable out 280 m, USNM No. 141621.

Allotype: Adult female, TL 1.56 mm, PUR 3.87:1, right furcal ramus length 0.090 mm, width 0.080 mm, from same sample as male. USNM NO. 141622.

Paratypes: 5♂, 5♀ from same sample. USNM No. 141623.

Reference specimens: 2♂, 2♀, Lusiad V stn. 76, lat. 02°01′S, long. 91°58′E, 24 Apr. 1963, 1-m net, oblique tow, maximum cable out 280 m. USNM No. 141625. 2♂, 2♀, Capricorn stn. 2, lat. 02°54′N, long. 168°40′E, 28 Nov. 1952, 1-m net, oblique tow, maximum cable out 200 m. USNM No. 141624.

Distribution

P. morii was found primarily at Indian and Pacific Ocean localities distributed in a zonal band lying roughly between lat. 20°N and 20°S (Figure 12). Occurrences at higher latitudes are few and mostly in the vicinity of western boundary currents; e.g., in the Kuroshio Current region just east of Japan and east of southern Africa in the region of the Mozambique and Agulhas Currents. In the eastern

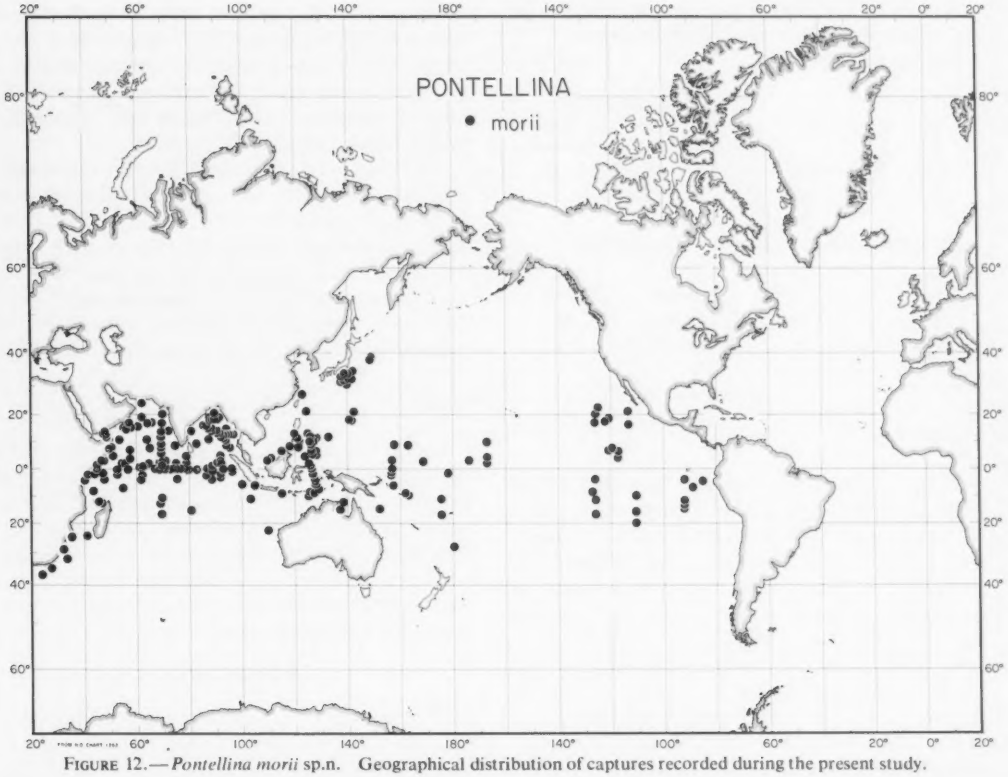

FIGURE 12.—*Pontellina morii* sp.n. Geographical distribution of captures recorded during the present study.

Pacific *morii* approached the Americas in the vicinity of Baja California and also at the latitudes of the Gulf of Guayaquil.

Among the 72 quantitatively analyzed samples containing *morii* estimates of abundance ranged from 0.003 to 0.5 individuals per m^3, the median being 0.01. In the sets of samples selected for quantitative analysis (Figure 1b) mean abundance in the Indian Ocean exceeded 0.04 individuals per m^3, 5 or more times higher than that found in sets of samples from the Pacific Ocean (Figure 35, Table 14); frequency of occurrence in the Indian Ocean (~30%) was also higher than in the Pacific Ocean ($\leq$20%).

PONTELLINA SOBRINA SP.N.

(Figures 13 and 14)

Specimens seen: 421 adult females, 364 adult males.

Standard measurements: specimens randomly selected from locations spanning the observed geographical distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.57	1.42-1.78	0.0134	50
Male	1.41	1.18-1.64	0.0118	56

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.73:1	3.17-4.16:1	33
Male	3.43:1	3.06-3.75:1	51

Diagnosis

Female

Most similar in appearance to *morii*. Spiniform process strongly demarcated from ThIV-V corner and typically symmetrical as in *morii*, but spine almost twice as long (Figure 10, Table 2); in dorsal view weakly curved spines extending posterolaterad (Figure 13g). Genital segment with two lateral clusters of hairs on both sides, anterior cluster consisting of fine hairs, posterior cluster consisting of coarse hairs (Figure 13 a, g); posterior margin of segment with border of long fine hairs as in all preceding species.

Male

ThIV-V (Figure 14a, b) as in female. P5 (Figure 14c, d) most similar to that in *morii* with notable differences present in chela. Distal segment of chela relatively long, apex extending beyond apex of laterodistal digitiform process of proximal segment. Moreover, distal segment lacking subapical spur (Figure 14c, d); in lateral view posterior basal process and digitiform process of proximal segment separated by rounded notch (Figure 14d); proximal segment in posterior view as in *morii*. Left P5 with Re1 longer than that in *plumata* (see Figure 30).

Additional Description

Female

Right furcal ramus somewhat shorter relative to its width as well as to length of prosome (see Figures 25, 27), median ratio of right furcal ramus length to width 1.12:1, range 1.02-1.31:1, 66 specimens; lateral edge of right ramus usually with broad point immediately anterior to base of outermost seta (Figure 13h), glandular tissue within ramus as in *plumata*.

P5 (Figure 13i) similar to that in *morii* except that ratio of lengths of exopod to endopod tends to be smaller, median 1.29:1, range 1.07-1.50:1, 52 specimens (see Figure 29); Ri typically with two relatively equal apical spines (see Table 7).

Attached spermatophore observed in 27 specimens (see Table 5), not differing appreciably in general features from those observed in *morii*.

Male

Right furcal ramus similar to that in *morii* in both relative length (see Figure 26) and in proportion of length to width, median 1.88:1, range 1.71-2.07:1, 40 specimens (see Figure 28); Re1 of left P5, compared to length of right furcal ramus, relatively longer than that in *morii* (see Figure 30), this ratio in *sobrina* ranging from 0.96-1.17:1, 21 specimens.

Etymology

The name *sobrina*, Latin for cousin, was chosen to acknowledge the close morphological relationship to *morii*.

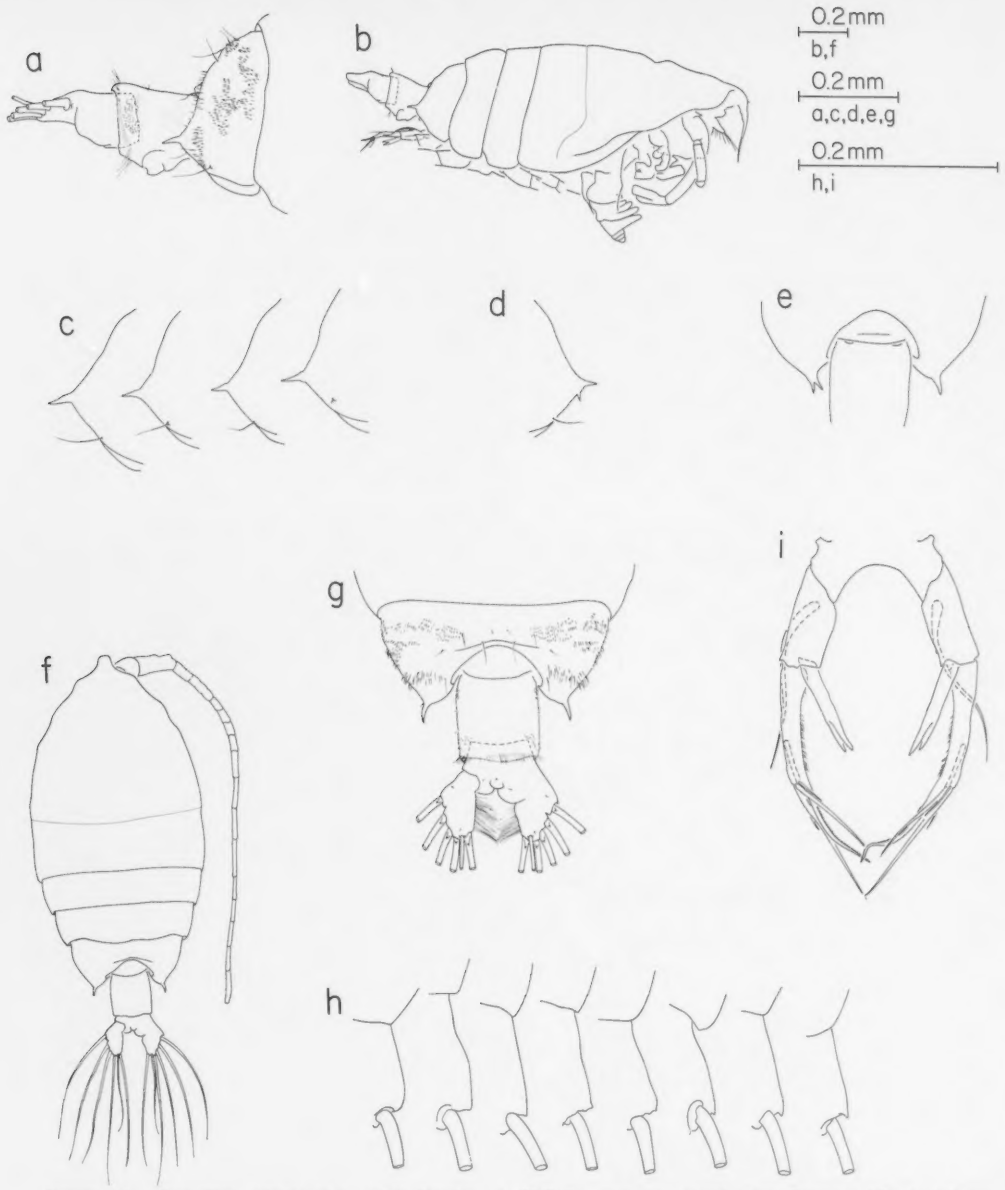

FIGURE 13.—*Pontellina sobrina* sp.n., adult female: **a.** ThIV-V, urosome, lateral view (Bonacca 35); **b.** habitus, lateral view (same as **a**); **c.** variation in ThIV-V spine, lateral view (left to right: EASTROPAC *Jordan* 037; 2 specimens Bonacca 31, Shellback 51); **d.** variation in left ThIV-V, lateral view, specimen with two spines (Bonacca 50); **e.** variation in left ThIV-V, dorsal view (La Creuse OT-6); **f.** habitus, dorsal view (same as **a**); **g.** ThIV-V and urosome, dorsal view (same as **a**); **h.** variation in lateral margin of right furcal ramus, dorsal view (left to right: La Creuse OT-6; La Creuse 18; La Creuse OT-14; La Creuse 17; La Creuse OT-14, different specimen; 2 specimens La Creuse 18; Bonacca 33); **i.** P5, anterior view (same as **a**).

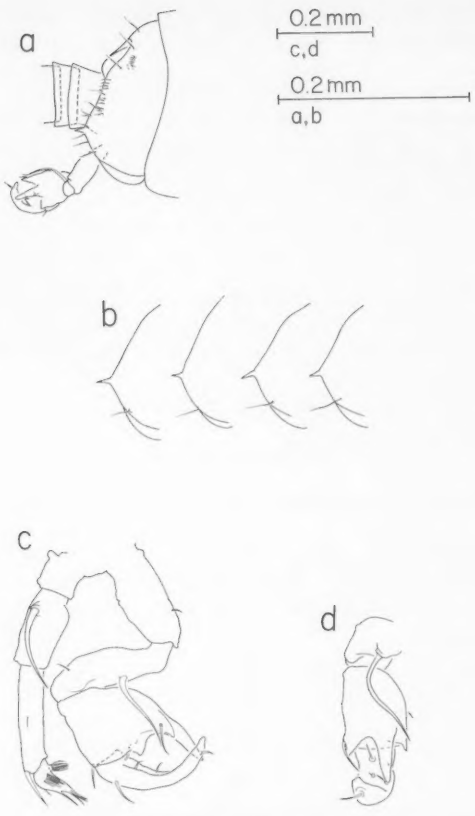

FIGURE 14.—*Pontellina sobrina* sp.n., adult male: **a.** ThIV-V, part of urosome and P5, lateral view [TO-58-1 (Scot) 33]; **b.** variation observed in ThIV-V spine, lateral view (left to right: Bonacca 55; Bonacca 43; 2 specimens Bonacca 51); **c.** P5, posterior view (La Creuse 21); **d.** chela P5, lateral view (Shellback 51).

Types

Holotype: Adult male, TL 1.42 mm, PUR 3.44:1, sorted from plankton sample taken at Bonacca stn. 51, lat. 13°44′N, long. 90°51′W, 19 Aug. 1963, ½-m net, oblique tow, maximum cable out 200 m. USNM No. 141617.

Allotype: Adult female, TL 1.52 mm, PUR 3.75:1, right furcal ramus length 0.080 mm, width 0.075 mm, from same sample as male. USNM No. 141618.

Paratypes: 5♂, 5♀ from same sample. USNM No. 141619.

Reference specimens: 5♂, 5♀, La Creuse stn. 15, lat. 08°41.2′N, long. 79°31.2′W, 4 May 1962, GV net towed between 0 and 4 m. USNM No. 141620.

Distribution

P. sobrina is obviously indigenous to the eastern tropical Pacific Ocean (Figure 15). The species was found only at Pacific stations east of long. 130°W. Occurrences at latitudes higher than 20° were restricted to a few samples taken near the mouth of the Gulf of California. Thus, the apparent boundaries coincide in general with the North and South Equatorial Currents, and its westernmost limits lie in the path of the Equatorial Countercurrent.

In 31 quantitative samples containing *sobrina* abundance varied from 0.01 to 0.66 individuals per m^3, the median being 0.04. In the sets of samples selected for quantitative analysis (Figure 1b) *sobrina* showed mean abundance values (ranging from 0.02 to 0.09 individuals per m^3) similar to those of *morii* in the Indian Ocean and to *plumata* outside of the eastern tropical Pacific (see Figure 35, Table 18).

DEVELOPMENTAL STAGES AND BREEDING

Immature specimens of *Pontellina* were sorted routinely together with adults. They were neither as abundant nor as frequent as the adults, a difference that is at least partially attributable to escapement of younger stages through the relatively coarse mesh (~0.5 mm) of most of the nets used to obtain our samples. General *Pontellina* habitus characteristics such as appearance of the prosome in dorsal view, rostrum, strong Mx2, and relatively long setae on A2 and Mnd served to distinguish the specimens. The number of swimming legs and body segments as well as total body length were used to determine their ontogenetic stage. Identification to species was reasonably certain only for stage V copepodids; details are presented below. Specimens of stages III and IV were tentatively assigned to species on the basis of their geographical origin. The following

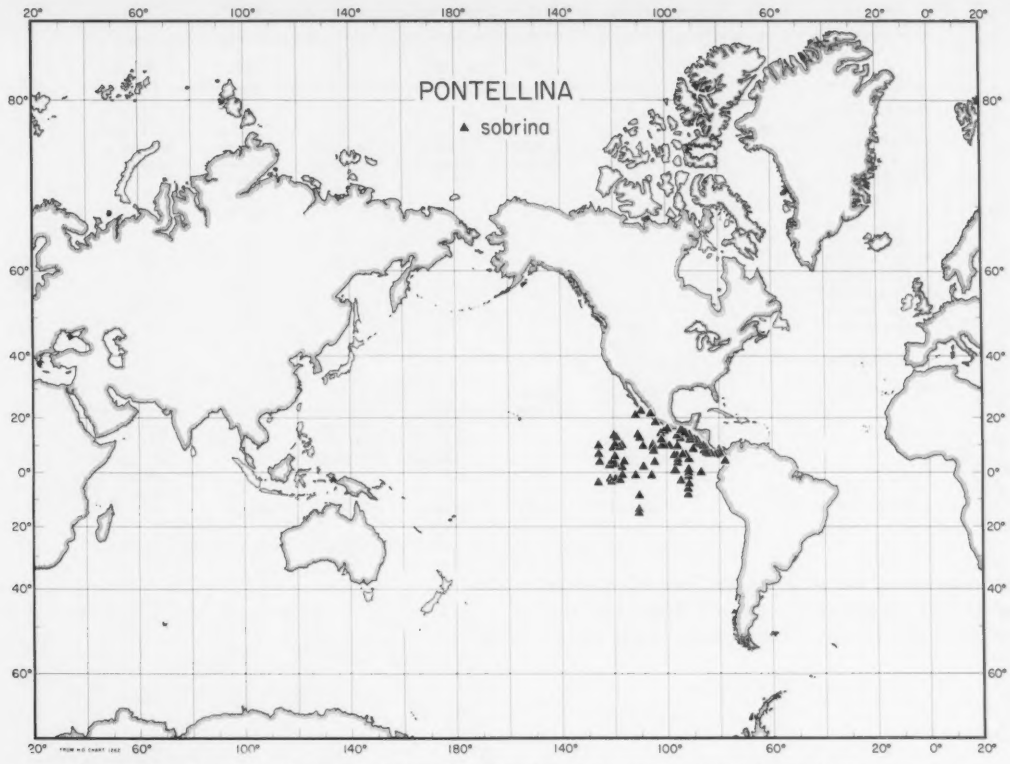

FIGURE 15.— *Pontellina sobrina* sp.n. Geographical distribution of captures recorded during the present study.

notes and Table 3 summarize ontogenetic characteristics of stages II through V prevailing in the genus.

Stage II

TL 0.72-0.76 mm (5 specimens). Rostral filaments and dorsal ocelli-like structures present; prosome with 4 free segments, urosome with 2 segments. Re of P1 and P2 bimerous, Ri of P1 and P2 and both rami of P3 unimerous, P4 consisting of a pad with folds, short setae and an incipient Ri; P5 lacking.

Stage III

(Figure 16c)

TL 0.82-0.88 mm (20 specimens). Neither sexes nor species distinguishable. Prosome with 5 segments, urosome with 2 segments. Re of P3 bimerous, Ri of P3 as well as both rami of P4 unimerous. P5 lobiform, bearing one apical seta.

Stage IV Female

(Figure 16a)

TL 0.90-1.10 mm (22 specimens, probably including all four species). Urosome with 3 segments. Re of P3 and P4 bimerous, Ri unimerous. Re of P5 unimerous; right Re and elongate seta on mediodistal corner of Re slightly larger than those of left P5; Ri lobiform, incompletely separated from B2.

Stage IV Male

(Figure 16b)

TL 0.95-1.10 mm (22 specimens, probably including all four species). Male resembles

TABLE 3.—Ontogenetic development in copepodite stages of *Pontellina*.

	II	III	IV♂	IV♀	V♂	V♀
Thoracic segments	4	5	5	5	5	5
Free abdominal segments	2	2	3	3	4	3
Rostral filaments	present	present	present	present	present	present
Dorsal ocelli	present	present	present	present	present	present
Right A1					segments 13-16 swollen	
P1 Re segments	2	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P2 Re segments	2	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P3 Re segments	1	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P4 Re segments	lobe, 1 seta	1	2	2	3	3
Ri segments	lobe, 1 seta	1	1	1	2	2
P5 Re segments	absent	lobe, 1 seta	1 right leg slightly larger than left	1 right leg slightly larger than left	2 right leg larger than left	1 right leg with 5 setae, left leg with 6 setae
Ri segments	absent	absent	rudimentary	1	absent	1

corresponding stage of female, but P5 with Ri absent or appearing as a small distal swelling on B2. Right Re also slightly larger than left.

Stage V Female

(Figure 17a-l)

TL 1.18-1.48 mm (40 specimens, all species represented). ThIV and V almost completely separated. Urosome with 3 segments, genital segment largest and with weak ventral swelling. Furcal rami incompletely separated from anal segment. Lateral margin of right furcal ramus proximal to first seta lacking protrusion. Left and right A1 symmetrical. Re of P3 and P4 trimerous, Ri bimerous. P5 with proportions of Re and Ri showing similarity to those of adult. Re unimerous with 5 setae on right leg, 6 setae on left leg; proximal Si of left side notable for its size and curved shape, an asymmetry lacking in the adult.

Stage V Male

(Figure 18a-q)

TL 1.20-1.44 mm (40 specimens, all species represented). ThIV and V almost completely separated. Urosome with 4 segments. Furcal rami incompletely separated from anal segment.

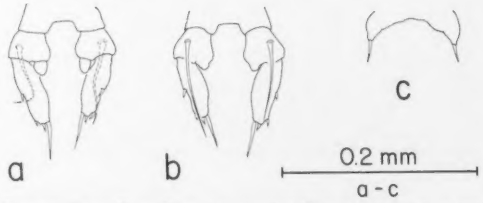

FIGURE 16.—*Pontellina* sp. copepodite stages: **a.** stage IV female, P5, anterior view; **b.** stage IV male, P5, posterior view; **c.** stage III copepodid, P5.

Right A1 with segments 13-16 slightly swollen, segments distal to swelling partly fused. P5 trimerous, slightly curved medially; right leg longer than left leg, Ri not developed.

In other genera of Pontellidae, as well as in a number of other heterarthrandrid families (Diaptomidae, Temoridae, Centropagidae, Pseudodiaptomidae) we note that fusion of urosomal segments I and II in the female first appears in the stage V copepodid (Gurney, 1931; Johnson, 1935; Crisafi, 1960; Lawson and Grice, 1970; Grice, 1971). Morphological features of the genital plate, antrum, and internal structures such as the seminal receptacles (Fahrenbach, 1962; Frost and Fleminger, 1968) are lacking in the stage V female. We also note that in most amphascandrid families (e.g., Calanidae, Para-

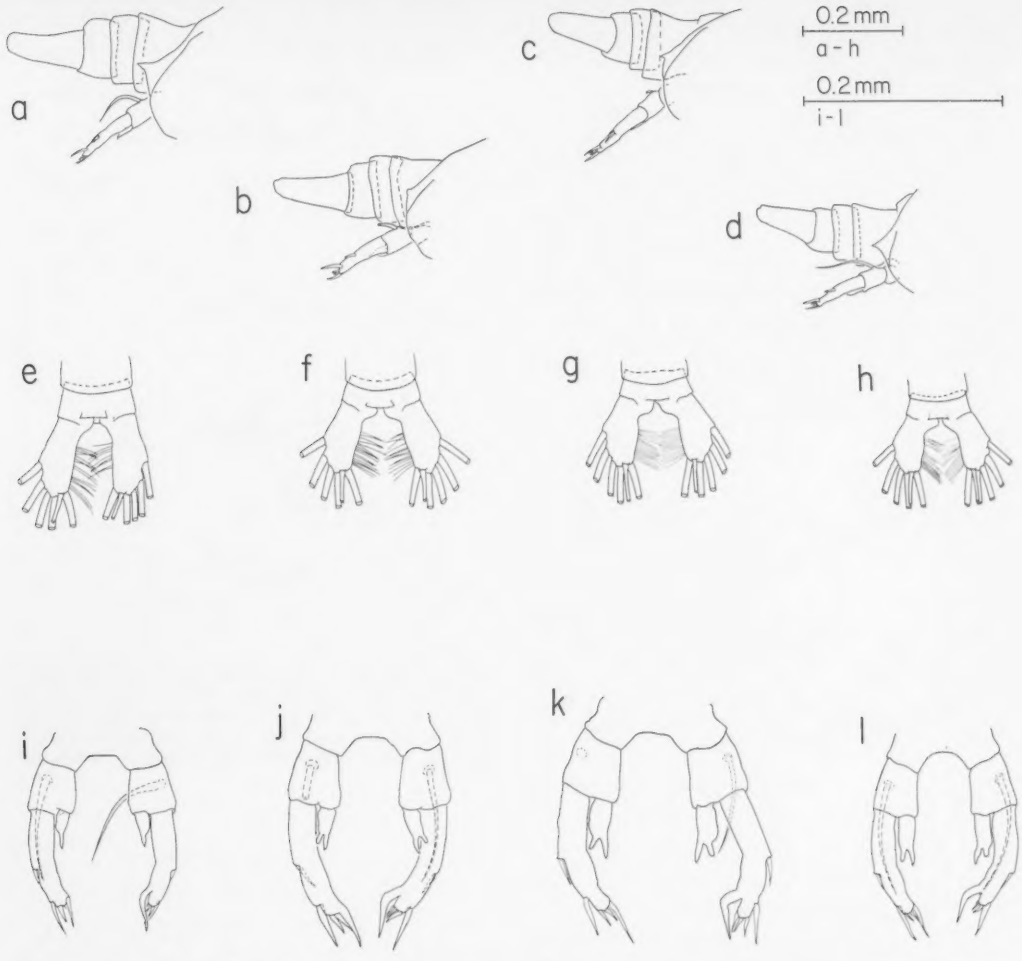

FIGURE 17.—Copepodite stage V, females: **a-d.** ThIV-V, right P5 and urosome, lateral view; **e-h.** anal segment, furcal rami, dorsal view; **i-l.** P5, anterior view. *Pontellina plumata:* **a, e** (*Atlantis II*-31-1); **i** (Lusiad V-60). *P. platychela:* **b, f, j** (*Atlantis II*-20-42). *P. morii:* **c, g, k** (Dodo VI, near Mombasa Harbor). *P. sobrina:* **d, h, l** [TO-58-1 (Scot) 56].

calanidae, Pseudocalanidae, Aetideidae, Euchaetidae, Phaennidae, Scolecithricidae) but not in Eucalanidae (Johnson, 1937; Sewell, 1929; Björnberg, 1967; and our unpublished observations of all species) fusion of urosomal segments I and II seems to be delayed until the appearance of the sexually mature female. This pattern has been documented by a number of ontogenetic studies on individual species (With, 1915; Nicholls, 1934; Campbell, 1934; Marshall and Orr, 1955; Matthews, 1964; and our unpublished observations).

Notes on Individual Species

Pontellina plumata
(Figures 17a, e, i; 18a, e, i, m, p)

Copepodite stage V female: TL $\bar{x}$ 1.38 mm, range 1.26-1.48 mm, 10 specimens. Posterolateral corner of ThV (Figure 17a) produced into a strong point similar to the adult. Furcal rami symmetrical (Figures 17e, 19), length of right ramus relative to width greater than that in *morii* (Figure 20). P5 Ri shorter than in *morii*

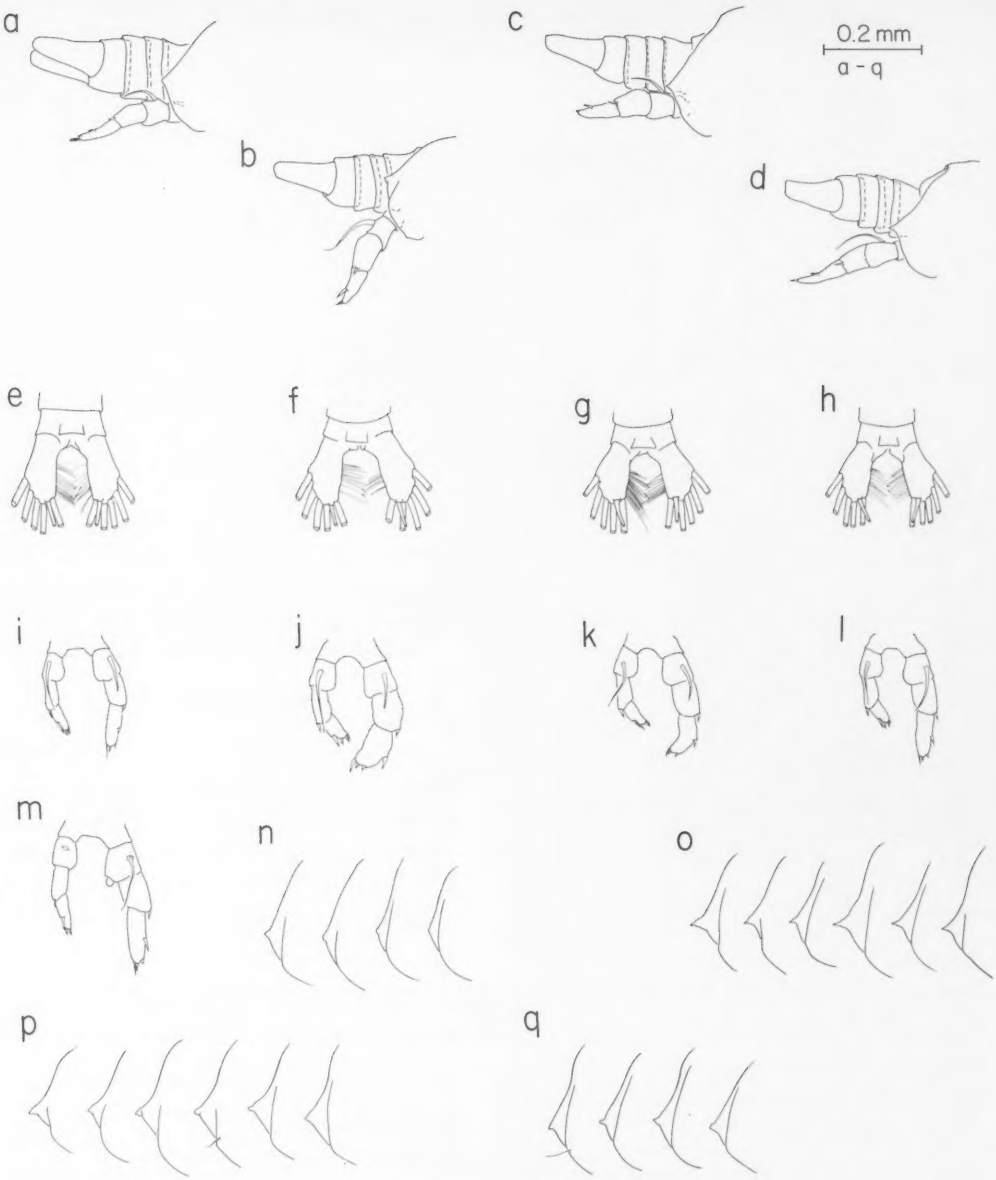

FIGURE 18.—Copepodite stage V, males: **a-d.** ThIV-V, right P5 and urosome, lateral view; **e-h.** anal segment, furcal rami, dorsal view; **i-m.** P5, posterior view; **n-q.** range of variation in ThIV-V, lateral view. *Pontellina plumata:* **a, e, i** (Lusiad V-43); **m** (Monsoon 2, atypical P5 with Ri); **p** (left to right: *Atlantis II*-31-74; *Atlantis II*-31-7; *Atlantis II*-31-28; *Atlantis II*-31-23; *Gascoyne* G1/32/63; Troll 25A). *P. platychela:* **b** (*Atlantis II*-31-60); **f, j** (*Atlantis II*-31-15); **n** (left to right: *Oregon* 1289; *Atlantis II*-31-50; *Atlantis II*-20-42; *Atlantis II*-31-57). *P. morii:* **c, g, k** (Lusiad V-43); **q** (left to right: EQUAPAC *Horizon* 31; Lusiad V-68; *Anton Bruun II*-58; *Anton Bruun I*-60). *P. sobrina:* **d, h, l**: La Creuse 18); **o** [left to right: EASTROPAC *Rockaway* 064; TO-58-1 (Scot) 29; TO-58-1 (Scot) 38; EASTROPAC *Rockaway* 071; TO-58-1 (Scot) 36; EASTROPAC *Rockaway* 056].

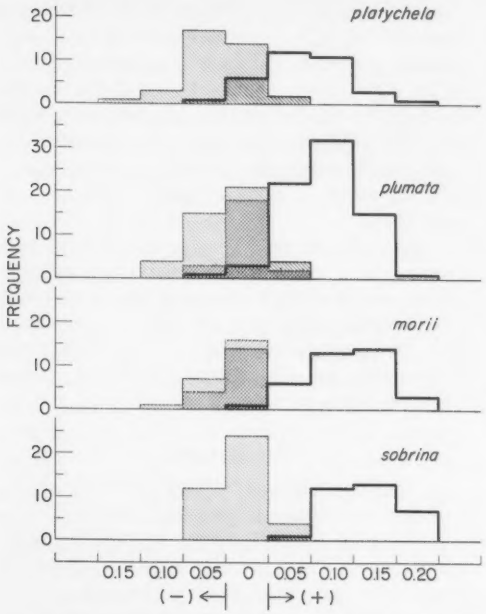

FIGURE 19.—Frequency distribution of differences in length of left furcal ramus and right furcal ramus for the four species of *Pontellina*. Gray with heavy outline = adult females; left-diagonal hatch with light outline = adult males; right-diagonal hatch with dotted outline = stage V females.

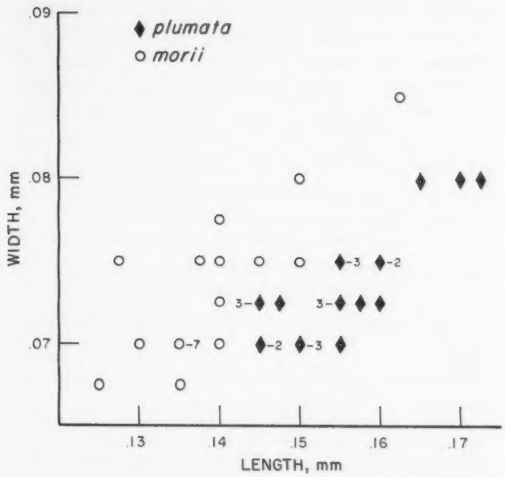

FIGURE 20.—Width of right furca (ordinate) plotted against length (abscissa) for female stage V copepodids of *Pontellina plumata* and *P. morii*.

relative to length of right furcal ramus (Figure 21). Re to Ri length ratio, median 3.0:1, range 2.3-3.5:1, 19 specimens (Figure 22); left P5 with medialmost seta on Re small and gently curved (Figure 17i) relative to that in *morii* (Figure 17k).

Copepodite stage V male: TL $\bar{x}$ 1.30 mm, range 1.20-1.44 mm, 10 specimens. Posterolateral corner of ThV ending in a broad point (Figure 18a, p). Terminal segment of right P5 about 3.1 times longer than wide (Figure 18i), endopod rarely present (Figure 18m). Furcal rami (Figure 18e) similar in relative length and width to those of female.

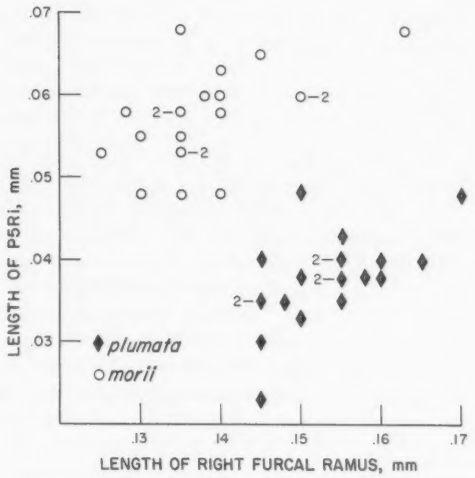

FIGURE 21.—Length of P5 Ri (ordinate) plotted against length of right furcal ramus (abscissa) for female stage V copepodids of *Pontellina plumata* and *P. morii*.

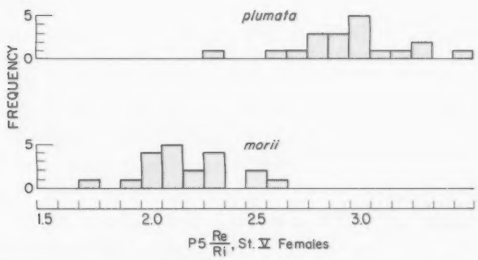

FIGURE 22.—Frequency distribution of P5 Re:Ri ratio for female stage V copepodids of *Pontellina plumata* and *P. morii*.

Pontellina platychela
(Figures 17b, f, j; 18b, f, j, n)

Copepodite stage V female: TL $\bar{x}$ 1.37 mm, range 1.18-1.46 mm, 10 specimens. ThV posterolateral corners rounded and ending in a small denticle (Figure 17b) as in adult. Furcal rami (Figure 17f) and P5 (Figure 17j) resembling those of *plumata*.

Copepodite stage V male: TL $\bar{x}$ 1.30 mm, range 1.24-1.36 mm, 10 specimens. Margin of posterolateral corner of ThV with weak denticle (Figure 18b, n). P5 with distinctive right leg (Figure 18j), Re considerably broader than in the other three species, about 1.6 times as long as wide. Furcal rami (Figure 18f) as in *plumata*.

Pontellina morii
(Figures 17c, g, k; 18c, g, k, q)

(Notes based on specimens from localities in the Indian Ocean.)

Copepodite stage V female: TL $\bar{x}$ 1.28 mm, range 1.18-1.36 mm, 10 specimens. ThV corner typically with a small spiniform point (Figure 17c) resembling that in the adult. Ri of P5 (Figure 17k) longer than in *plumata* (Figure 21), typically with 2 spines; Re:Ri length ratio considerably less (median 2.1:1, range 1.7-2.6:1, 20 specimens) than in *plumata* (Figure 22). Furcal rami symmetrical (Figure 19), shorter than those in *plumata* (Figure 20), as in sexually mature stages. Medial setalike process of Re of left P5 (Figure 17k) more abruptly bent (~90°) than that of the other three species (Figure 17i).

Copepodite stage V male: TL $\bar{x}$ 1.21 mm, range 1.12-1.32 mm, 10 specimens. Posterolateral corner of ThV ending in a relatively short spiniform point (Figure 18c, q) about one-half the length of that in *sobrina* (Figure 18d, o) and much less robust than that in *plumata* (Figure 18a, p). Distal segment of right P5 distinctly bent mediad (Figure 18k). Furcal rami (Figure 18g) similar in relative length and width to those in female.

Pontellina sobrina
(Figures 17d, h, l; 18d, h, l, o)

(Notes based on juvenile specimens from easternmost Pacific localities which were accompanied by large numbers of adults; the localities are relatively distant from those yielding *morii*.)

Copepodite stage V female: TL $\bar{x}$ 1.25 mm, range 1.18-1.34 mm, 10 specimens. Differences between sexually immature *sobrina* and *morii* females are relatively weak, e.g., greater length of the ThV point (Figure 17d) and the weaker bend of the medial setalike process on the left Re of P5 (Figure 17l), appear to be useful, but lack confirmation by measurements from a geographically representative series of specimens.

Copepodite stage V male: TL $\bar{x}$ 1.25 mm, range 1.12-1.38 mm, 10 specimens. Posterolateral corner of ThV produced into a relatively long slender point (Figure 18d, o). Right P5 with straight distal segment resembling that in *plumata*, but all segments in P5 of *sobrina* appear slightly wider.

Sex Ratios

In laboratory-reared populations sex ratios among adult copepods of several families have been found to vary widely (for recent comments see Heinle, 1970; Katona, 1970; Paffenhöfer, 1970). In natural populations, however, late immature copepodids have been found to produce males and females in about equal numbers (Marshall, 1949). Among randomly sorted, sexually mature adults of the four species of *Pontellina* females consistently outnumbered males by roughly 1.3:1 (Table 4).

Assuming that the sexes are genetically one to one, the observed male-to-female ratios in *Pontellina* could be readily accounted for if females live longer than males, a likelihood suggested by many authors for various amphascandrid copepod genera. In a small series of rearing experiments on *Labidocera trispinosa*, A. Barnett (pers. comm., 1972) has found that following the adult moult females live 2 to 3 wk and males about 1 wk.

TABLE 4.—Frequency of sexually mature individuals and sex ratios in *Pontellina*.

Species	♀ N	♀ %	♂ N	♂ %	♀:♂	No. samples
platychela	[1]159	54	[1]137	46	1.16	72
plumata	1,259	58	917	42	1.37	531
morii	433	60	284	40	1.52	240
sobrina	421	54	364	46	1.16	113

[1] One sample, i.e., *Atlantis II* 20-42, was omitted because it provided the extremely disproportionate capture of 327 males and 10 females.

REMARKS ON SEASONAL OCCURRENCE AND BREEDING

Capture records alone do not necessarily disclose the distribution of the optimal habitat of a planktonic species (Fleminger, 1972), i.e., the region in which reproduction is usual, typically successful, and from which the progeny is likely to become entrained in a circulation system that ultimately provides new breeding stocks with suitable conditions for their offspring. Our sampling of *Pontellina* is incomplete for critical assessment of the impact of seasonal change on occurrence, geographical distribution, or reproduction. Moreover, as a consequence of the relatively large mesh sizes of the nets (see Table 15) sampling of most juvenile stages was not representative. Thus spermatophore occurrence on females is the only source of breeding information available to us.

In *Calanus*, spermatophores constitute evidence of mating within the past 48 h (Marshall and Orr, 1955). In other copepods, spermatophores are lost or shed soon after attachment; in *Labidocera trispinosa* discarding of the spermatophore has been observed to occur just prior to egg laying (G. Theilacker, pers. comm., 1970).

Few spermatophores were observed in *Pontellina* (Table 5) suggesting that as in *Calanus* they are not retained for an appreciable time after attachment. The 27 records of *sobrina* females bearing a spermatophore afford a glimpse of breeding patterns in that species. Spermatophore-bearing females appeared in February, May, and August samples. The localities span most of the latitudinal extent of *sobrina* captures on record, but all lie to the east of long. 98°W, and most are relatively close to the mid-American coast. In contrast, the few records of *morii* and *plumata* bearing spermatophores are widespread, suggesting that both species breed over a more extensive range in accordance with their more extensive geographical distributions.

PHYLOGENETIC RELATIONSHIPS AMONG THE *PONTELLINA* SIBLINGS

Dobzhansky (1972) stressed the heuristic value of sibling species when he pointed out " . . . sibling species permit the dissection of the process of speciation into studiable components." *Pontellina* appears especially well suited to explore the question of speciation in the planktonic biotope. Restriction to shallow tropical and subtropical oceanic waters apparently limits opportunities for complex diversity in planktonic calanoids (Fleminger and Hulsemann, 1973). The four species of *Pontellina* satisfy the number of suitable ranges that appear to be available within these biogeographical limits.

Three of these ranges reflect the geographically limited and relatively shallow lenses of Tropical Surface Water (Wyrtki, 1966, 1967) described from the eastern equatorial Pacific but also known on the basis of similar general features to prevail in the equatorial Atlantic Ocean (Muromtsev, 1963) and in the equatorial Indian Ocean (Wyrtki, 1971). The fourth range consists of the series of deeper lenses of warm water beyond Tropical Surface Waters and lying between the subtropical convergences in the Atlantic, Indian, and Pacific Oceans.

Pontellina's position as a distinctive genus is unchallenged, being strongly separated from its closest relative, *Pontellopsis*, in both morphology and habitat. Compelling evidence favoring consideration of the four populations of *Pontellina* as separate species is furnished by the morphological distinctions of each, their independent geographical distributions, and the morphological integrity of their diagnostic features. That is, despite widespread regions of geographical overlap where two or three of the species may be captured in the same net tow, no evidence of intergradation or hybridization has been observed.

Evidence of strongly regionalized habitat adaptation may be inferred from the apparent failure of each species to colonize areas occupied by its adjacent congener. Failure to colonize must be regarded as significant. All four species occur in surface layers (Wilson, 1942; Heinrich, 1961; Vinogradov and Voronina, 1964; Fleminger and Hulsemann, unpublished data) where air-sea interactions provide opportunity for dispersal and advection with neighboring circulation systems, but the distribution of each species overlaps at most only a portion of the range of its neighboring congeners.

TABLE 5.—Adult female specimens of *Pontellina* bearing a spermatophore.

Species	Sampling date	Latitude	Longitude	Station	Total length (mm)	Sac length (mm)
P. platychela	III-8-66	00°08'S	18°31'W	*Atlantis II*-20-42	1.66	0.490
P. plumata	VI-15-69	33°49'N	139°10'E	Scan IV-1	1.66	0.460
					1.76	0.460
	VI-6-52	01°00'S	112°24'W	Shellback 47	1.50	0.425
	III-30-69	21°54'S	110°02'W	Piquero V-49	1.56	0.365
P. morii	IV-19-68	05°11'N	123°58'E	Circe II-NT 11	1.58	0.420
	VII-2-52	05°18'S	85°04'W	Shellback 105	1.86	0.440
P. sobrina	II-12-67	00°28'N	92°02'W	EASTROPAC *Rockaway* 060	1.68	0.390
	V-12-58	07°22'N	92°47'W	Scot 46	1.56	0.360
					1.70	0.395
	V-4-62	08°41'N	79°31'W	La Creuse 15	1.40	0.340
					1.44	0.385
					1.46	0.370
					1.42	0.355
	V-7-58	09°45'N	96°04'W	Scot 35	1.62	0.410
	VIII-16-63	09°51'N	85°43'W	Bonacca 42	1.48	0.385
					1.46	0.320
	V-17-62	13°07'N	91°34'W	La Creuse OT-6	1.48	0.330
					1.50	0.355
	VIII-18-63	13°29'N	90°09'W	Bonacca 50	1.50	0.320
					1.62	0.360
					1.52	0.340
					1.48	0.340
	VIII-19-63	13°44'N	90°51'W	Bonacca 51	1.50	0.390
					1.52	0.340
	VIII-20-63	13°57'N	92°02'W	Bonacca 58*	1.54	0.390
					1.56	0.415
					1.48	0.355
					1.56	0.365
					1.50	0.375
					1.50	0.380
					1.52	0.395
					1.50	0.385

* One additional specimen was observed in this sample with a damaged spermatophore.

Morphology and distribution also support our conclusion that the four species are phylogenetically close and, in fact, comprise a monophyletic unit—or holophyletic in Ashlock's (1971) terminology—appearing to have been recently derived from a single tropical-subtropical epiplanktonic precursor (in preparation).

Our objective in this section is to examine the degree of similarity among the siblings as a basis for determining phylogenetic relationships. In the absence of a fossil record, inferences drawn from comparative morphology, geographical distribution, and essential habitat adaptation may provide a relative historical perspective for judging phylogeny within a taxon.

Phylogenetic relationships within *Pontellina* were judged both intuitively and objectively on the basis of characters that showed a cohesive pattern of similarity or dissimilarity. We concur with the rebuttals of Throckmorton (1965, 1968) and Voris (1971) to the views of orthodox numerical taxonomy in defense of the weighting of taxonomic characters: i.e., characters differ in their taxonomic usefulness, and the adaptive significance of these differences is not beyond logic and comprehension.

Throckmorton and Voris show empirically that characters are decidedly not equal in their content of phylogenetic information. Their operational method for character selection rests upon the direct and assumption-free advantages of *a posteriori* weighting of correlated sets of derived characters.

Judging from the numerous articles in Systematic Zoology, numerical taxonomic phylogenies derived from large numbers of unweighted characters do not vary from phylogenies implicitly or explicitly arranged by experienced workers employing sets of correlated adaptive characters.

Body Dimensions and Proportions

Total Length (TL)

Intraspecific sexual differences in TL are greater than interspecific differences; males are about 10% shorter than females (Table 6, Figure 23). In both sexes *morii* and *sobrina* are smaller than *platychela* and *plumata*. The difference between the mean TL of males or females of species belonging to the same pair is not significant. However, the difference between the mean TL of either species of one pair with that of either species in the other pair is highly significant in both sexes (Student's *t*-test). The overall difference is produced largely by the distance between the rostrum and the cephalic groove and the length of the furca (see below).

Prosome-Urosome Length Ratio (PUR)

In both sexes *morii* and *sobrina* occur at the high end of the PUR distribution (Table 6, Figure 24). In males, *morii* and *sobrina* have similar distributions at the high end of the

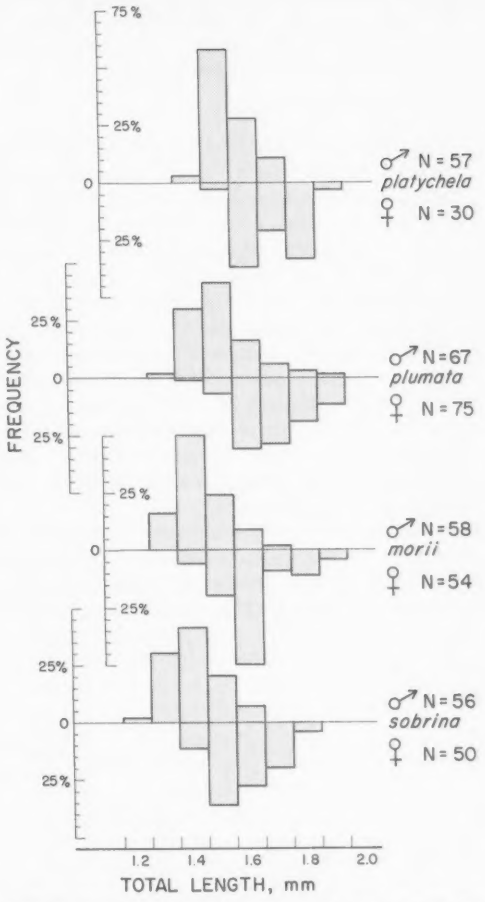

FIGURE 23.—Frequency distribution of total length for both sexes of the four species of *Pontellina*.

TABLE 6.—Total length (TL) and prosome-urosome length ratio (PUR) of *Pontellina* spp. adults; data from various geographical localities combined.

Species	TL (mm) $\bar{x}$	TL (mm) Range	TL (mm) $s_{\bar{x}}$	TL (mm) *N*	PUR $\bar{x}$	PUR Range	PUR $s_{\bar{x}}$	PUR *N*
Males:								
P. platychela	1.699	1.54-1.96	0.0173	30	3.438:1	3.19-3.89:1	0.0362	30
P. plumata	1.692	1.44-1.94	0.0126	75	3.282:1	2.92-3.72:1	0.0179	75
P. morii	1.608	1.38-1.88	0.0145	54	3.643:1	3.39-4.10:1	0.0360	35
P. sobrina	1.570	1.42-1.78	0.0134	50	3.732:1	3.17-4.16:1	0.0417	33
Females:								
P. platychela	1.556	1.41-1.74	0.0089	57	3.223:1	2.86-3.55:1	0.0228	49
P. plumata	1.511	1.34-1.92	0.0130	67	3.066:1	2.84-3.93:1	0.0243	52
P. morii	1.435	1.26-1.68	0.0100	58	3.339:1	2.87-3.73:1	0.0245	50
P. sobrina	1.406	1.18-1.64	0.0118	56	3.426:1	3.06-3.75:1	0.0235	51

range, *platychela* being intermediate and *plumata* occupying the low end. Females follow the same general pattern, but *morii* and *sobrina* show considerably less overlap.

Length of Furcal Rami

The length of both rami is directly related to prosome length as well as TL. Shortening and fusion of the right ramus in adult females introduces asymmetry but the change does not alter the essential relationship to body length. In the female sex (Figure 25) *morii* and *sobrina* occupy one side of the overall distribution of length of the right ramus, *platychela* and *plumata* the other with virtually no overlap between the two pairs of species. Males show more scatter (Figure 26) and apparent differences in allometry; *sobrina* and *morii* tend to diverge with respect to furcal length while *plumata* and *platychela* tend to diverge with respect to prosome length.

Examination of furcal length relative to furcal width increases separation of the three equatorial species. It also enhances separation of *platychela* and the Atlantic samples of *plumata* as well as separation of *morii* and the Indo-Pacific samples of *plumata* (Figure 27). A generally similar pattern is seen in the males (Figure 28) except that *morii* and *sobrina* overlap freely with respect to the furcal length: width ratio.

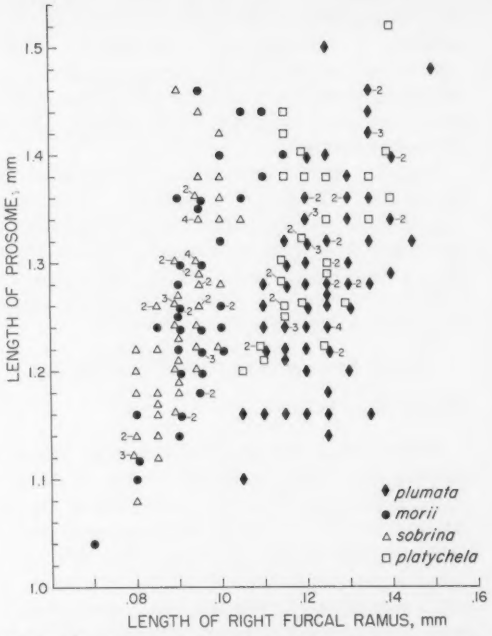

FIGURE 25.—Length of P (ordinate) plotted against length of right furcal ramus (abscissa) for females of the four species of *Pontellina*.

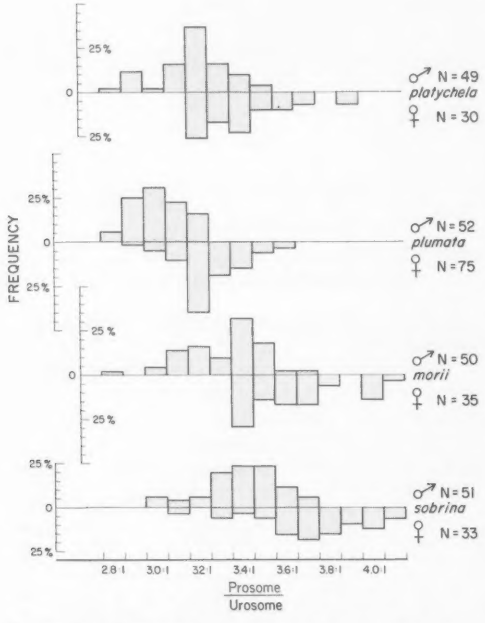

FIGURE 24.—Frequency distribution of P:U ratio for both sexes of the four species of *Pontellina*.

ThIV-V Posterior Spine

Strong sexual dimorphism appears in adults. Among the females, *plumata* is unique; the base of the posteriorly directed spine rises roughly at the level of the proximal margin of the genital segment, the spine is robust and broadly triangular in both dorsal and lateral views (Figure 3a, d-f). The spines in the three equatorial species are similar to each other in being diminutive and needlelike or dentiform. They differ primarily with respect to relative length of the spine (Figures 6a, c, g, h; 9a, c, e, f; 11; 13a, c, g).

The ThIV-V spine in males appears in three states: *plumata* exhibits a minute denticle that

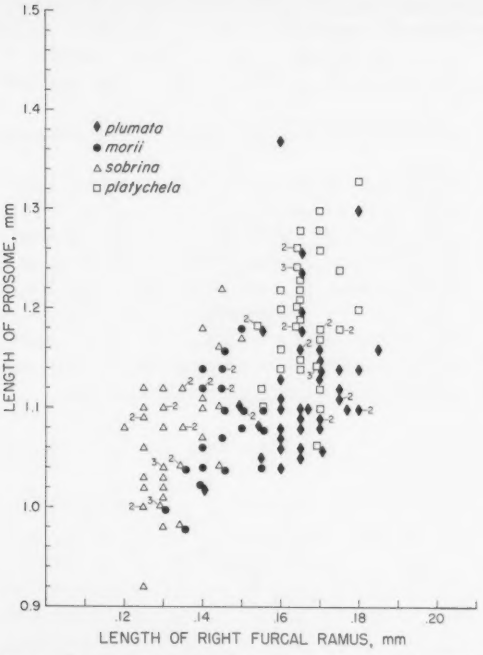

FIGURE 26.—Length of P (ordinate) plotted against length of right furcal ramus (abscissa) for males of the four species of *Pontellina*.

may be borne on a weakly produced boss; *morii* and *sobrina* bear a small spine resembling that found in the female of the species; *platychela* has no outgrowth whatsoever.

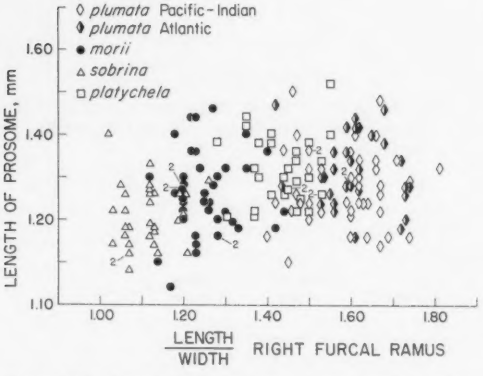

FIGURE 27.—Length of P (ordinate) plotted against length: width ratio of right furcal ramus (abscissa) for females of the four species of *Pontellina*.

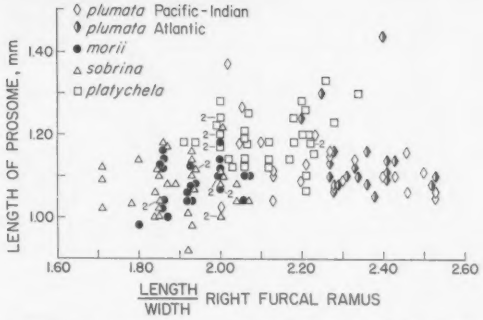

FIGURE 28.—Length of P (ordinate) plotted against length: width ratio of right furcal ramus (abscissa) for males of the four species of *Pontellina*.

Female Genital Segment

The distribution of lateral clusters of spinules provides the basis for distinguishing the different character states. Two species, *sobrina* and *plumata*, are similar in having two clusters on each side; *morii* has one cluster and *platychela* has none. There is preliminary evidence from examination with the scanning electron microscope (SEM), however, that the similarity of *plumata* with *sobrina* may in fact be superficial. Cluster size and spinule size differ even under the light microscope, and the SEM indicates the presence of fine sensoriiform filaments in *sobrina* and *morii*, but not in *plumata* or *platychela*. The SEM also revealed a second cluster consisting of minute denticles in *morii* anterior to the one visible with the aid of a light microscope (in preparation).

Female Fifth Pair of Swimming Legs

The two characters found in P5 that provide diagnostic information, i.e., the Re:Ri length ratio (Figure 29) and the distribution of spines on the endopod (Table 7) agree in showing strong similarity between *morii* and *sobrina* on the one hand and between *platychela* and *plumata* (all geographical sectors combined) on the other. It should be noted, however, that the similarity between *platychela* and *plumata* is weakened when the comparison is restricted to Atlantic Ocean samples of *plumata* (in preparation).

The distribution of the spines on the endopod is also noteworthy by virtue of the compelling

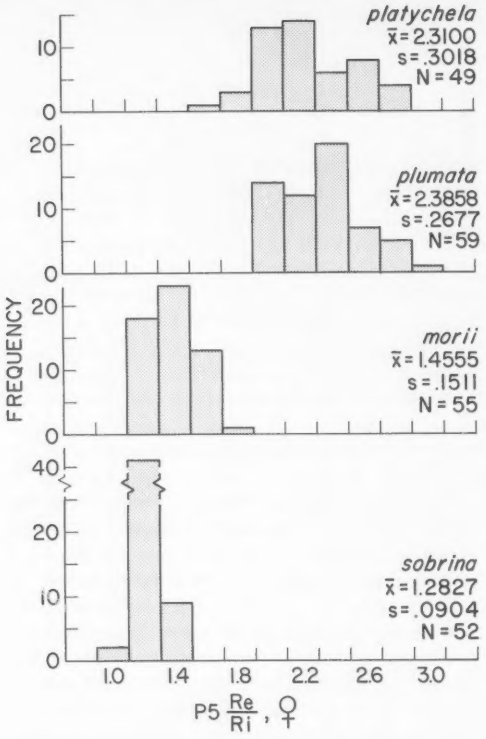

FIGURE 29.—Frequency distribution of P5 Re:Ri ratio for females of the four species of *Pontellina*.

evidence it provides in support of our judgment that the four siblings are valid species recently derived from the same parent species. The frequencies and widespread geographical occurrence of phenotypes are evidence of simple Mendelian inheritance and indicative of balanced polymorphism. Another pontellid, *Labidocera diandra*, has also been shown to be polymorphic (Fleminger, 1967b). In both *Pontellina* and *Labidocera* the apparent polymorphism affects a sexually modified appendage before the onset of maturity, the phenotypes being distinguishable in copepodite stage V. However, within its species group, only *L. diandra* displays the polymorphism which is visible in the male sex.

Male Fifth Legs and Right First Antenna

Segment lengths of sexually modified appendages that we examined tend to vary directly with prosome length. We chose the length of the right furcal ramus (Figure 25) instead of the prosome as our standard body length reference for comparing morphometry of sexual appendages because the furcal ramus length yielded graphic presentations with considerably less scatter within each sample.

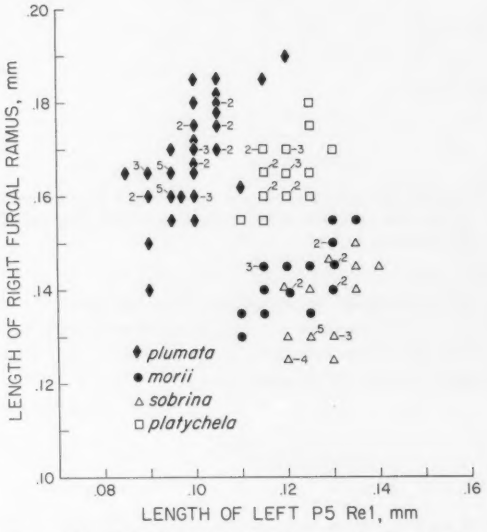

FIGURE 30.—Length of right furcal ramus (ordinate) plotted against length of left P5 Re1 (abscissa) for males of the four species of *Pontellina*.

TABLE 7.—Frequencies (%) of phenotypes varying in the number of spines on the endopod of the fifth pair of swimming legs in *Pontellina* spp. females.

Species (*N*)	Left leg: 1 spine Right leg: 1 spine	1 spine 2 spines	2 spines 1 spine	2 spines 2 spines
platychela (100)	34	16	12	38
plumata (300)	37	12	16	34
morii (200)	1	2	1	96
sobrina (100)	0	1	0	99

TABLE 8.—Dimensions of selected segments of sexually modified appendages of *Pontellina* spp. adult males.

Segments and species	$\bar{x}$(mm)	s	N	Range (mm)
Left P5 Re1 length:				
platychela	0.1193	0.0048	21	0.110-0.130
plumata	0.0988	0.0067	48	0.085-0.120
morii	0.1221	0.0079	19	0.110-0.130
sobrina	0.1269	0.0060	21	0.120-0.140
Right P5 Re1 width:				
platychela	0.1895	0.0109	20	0.170-0.210
plumata	0.1647	0.0112	47	0.140-0.195
morii	0.1960	0.0091	20	0.180-0.215
sobrina	0.1814	0.0098	21	0.165-0.200
A1 segment 18 length:				
platychela	0.3417	0.0152	26	0.300-0.365
plumata	0.3364	0.0220	32	0.285-0.400
morii	0.3063	0.0159	31	0.280-0.340
sobrina	0.3014	0.0137	29	0.280-0.335

Length of Left First Exopodal Segment

This segment is much shorter in *plumata* than in the other three species (Figure 30, Table 8). Small differences appear among the three equatorial species but they are inconspicuous in comparison to their distribution as a group relative to that of *plumata*.

Width of Right First Exopodal Segment

As in the section above on the left, Re1, the distributions of the three equatorial species broadly overlap, but *plumata* tends to be appreciably smaller (Figure 31, Table 8).

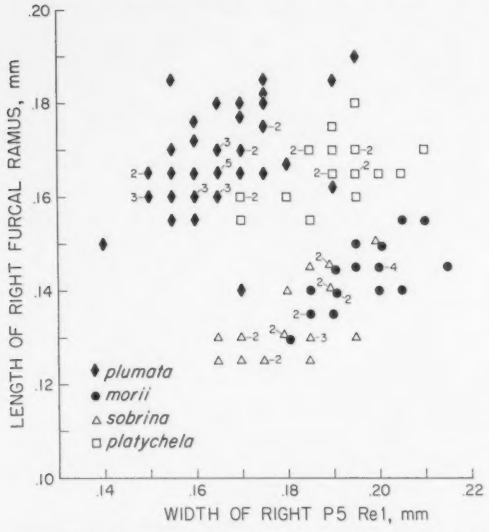

FIGURE 31.—Length of right furcal ramus (ordinate) plotted against width of right P5 Re1 (abscissa) for males of the four species of *Pontellina*.

Morphology of Right First Exopodal Segment

The proximal segment of the chela appears in three essential states: the swollen condition of *platychela* (Figure 7a, b), the slender condition of *plumata* (Figure 4i, j) and the slender condition characterized by a more distal position of the posterolateral outgrowth shared by *morii* and *sobrina* (Figures 11d, e; 14c, d).

Morphology of Right Second and Third Exopodal Segments

The distal segment of the chela appears in three states: the swollen condition of *platychela* (Figure 7b), the shortened, spurred condition of *morii* (Figure 11d, f) and the simple attenuated condition shared by *plumata* and *sobrina* (Figures 4j, 14d).

Length of Segment 18, Right First Antenna

Two siblings, *plumata* and *platychela*, broadly overlap and occupy the upper half of the overall distribution; the other two, *morii* and *sobrina*, broadly overlap in the lower half of the distribution (Figure 32, Table 8).

Spermatophore Attachment

(Figures 33, 34)

The three equatorial species agree in having

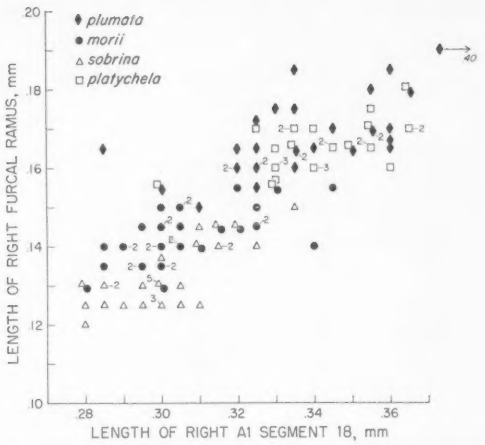

FIGURE 32.—Length of right furcal ramus (ordinate) plotted against length of segment 18 of right A1 (abscissa) for males of the four species of *Pontellina*.

the proximal end of the sac cemented to the right side of the genital segment, *morii* and *sobrina* in a virtually identical fashion, differing somewhat from the condition found in *platychela*. In *plumata*, however, attachment is restricted to the proximal end of the neck, the remainder of the neck and the entire sac hanging free from the body but showing helical convolutions similar to those present in the other congeners.

Geographical Occurrence

Three of the species, *morii*, *sobrina*, and *platychela*, were found primarily in low latitudes between 20°N and 20°S (Figures 8, 12, 15). The three species are essentially allopatric to one another, each predominating in a geographically different segment of equatorial circulation in the world's oceans (see Table 20). Relatively high frequencies of abundance or occurrence coincided with eutrophic equatorial regions characterized by a shallow O_2 minimum layer (≤ 1 ml/liter) lying at or near the permanent thermocline. The three species tend to concentrate in the uppermost 20 to 30 m of depth and virtually disappear below 50 m (in preparation).

The fourth sibling, *plumata*, is widespread in subtropical latitudes (Figure 5) and may be locally abundant in tropical regions downstream from areas of persistent upwelling. It is the only species of the genus with a circumglobal range but tends to be infrequent to absent in tropical areas dominated by its equatorial cognates (see Table 20). Its vertical distribution appears to encompass the surface to 200-m depth in subtropical latitudes, the lower limit shoaling to about 100 m in tropical latitudes (in preparation).

Summation of Phylogenetic Similarities

Thus within the framework of the 17 characters considered above, *morii* and *sobrina* show the highest frequency of similar character states. In practice their overall morphological similarity is sufficient to require routinely close inspection at appreciable magnifications for reliable separation. Though the next most frequently linked pairing, *plumata* and *platychela*, show similarity in about 60% of the features in Table 9, at low magnifications under a stereomicroscope they are almost as distinct from one another as each is from *morii* or *sobrina*.

As noted in the calanoid genera, *Labidocera* and *Clausocalanus* (Fleminger 1967b; Frost and Fleminger, 1968), the distinguishing features of the sibling species in *Pontellina* are limited to sexually modified characters, i.e., the fifth legs, the genital segment, the posterior corner of ThIV-V, the male right A1, and the caudal furca.

There is reason to regard *plumata* as retaining the strongest similarity to the *Pontellina* ancestral stock. This view rests upon two features: the slightly stronger resemblance of sexually modified structures in *plumata*, especially the ThIV-V spine in the female, to those of *Pontellopsis* and of the more eurytopic circumglobal distribution of *plumata* in comparison to the restricted distributions of its equatorial congeners.

To examine the statistical significance of the phylogenetic relationships inferred from the characters given in Table 9 we have utilized a computer program that detects significant levels of co-occurrence among sets of overlapping functions. The program has been informative in the detection of communities as well as in systematic classifications of flexibacteria (Fager, 1969).

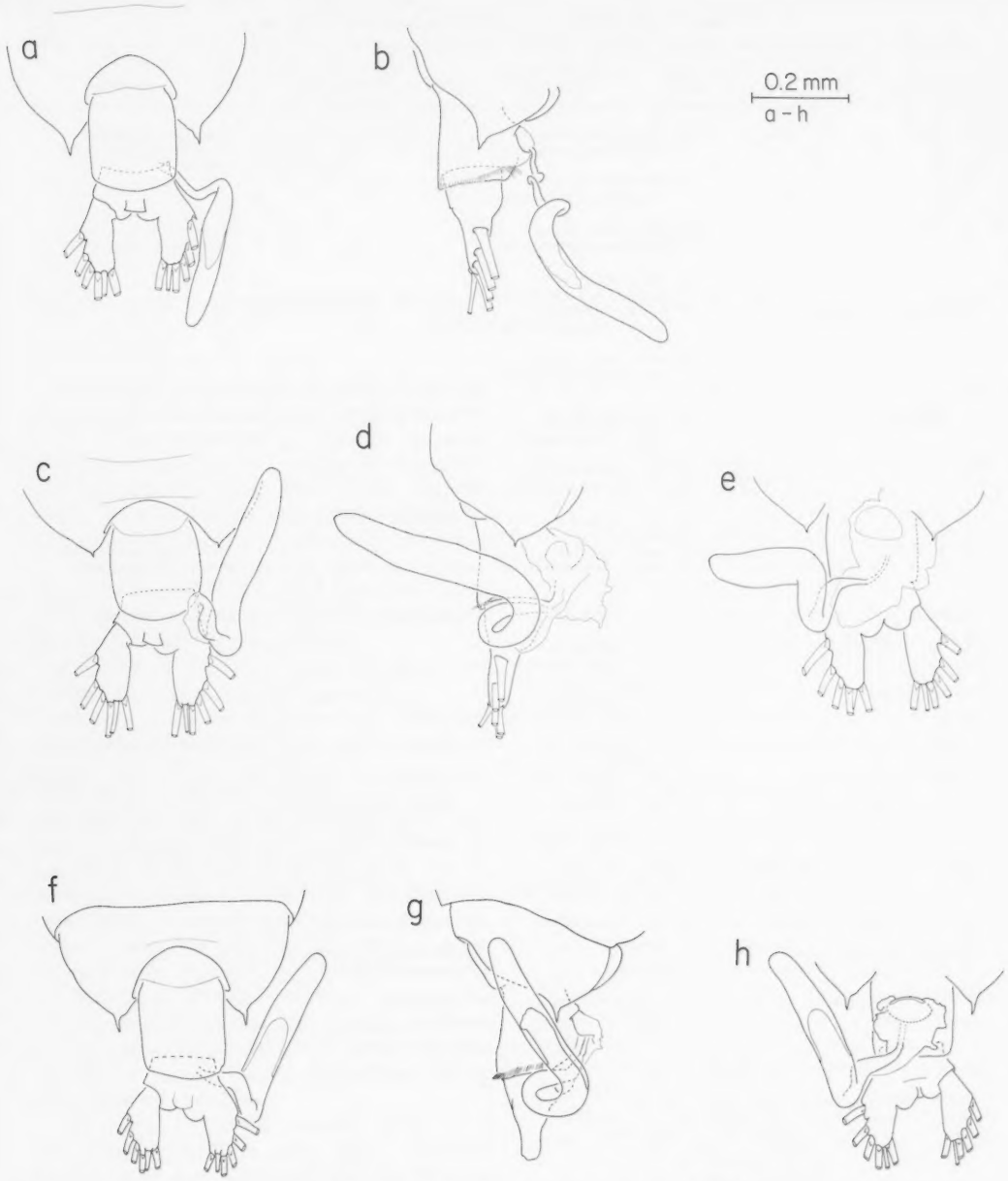

FIGURE 33.—ThIV-V and urosome of female with attached spermatophore. **a, b.** *Pontellina plumata.* **c-e.** *P. platychela.* **f-h.** *P. morii.* **a, c, f** dorsal view; **b, d, g** lateral view; **e, h** ventral view.

TABLE 9.—Shared character states among species of *Pontellina*.

Character	No. of states	Species sharing same state	Species with unique character state	Remarks
1. $\bar{x}$TL ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		Significant differences produced by furcal ramus length
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
2. PUR ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		Significant differences produced by furcal ramus length
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
3. Furcal ramus length ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
4. Furcal ramus length:width ratio ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
5. Th IV-V ♀	2	*morii*, *sobrina*, and *platychela*	*plumata*	
6. Th IV-V ♂	2	*morii* and *sobrina*; *plumata* and *platychela*		Minor differences between *plumata* and *platychela* ignored
7. Genital segment ♀	3	*plumata* and *sobrina*	*platychela*; *morii*	SEM results ignored
8. P5 ♀, Re:Ri ratio	2	*morii* and *sobrina*; *plumata* and *platychela*		
9. P5 ♀, Ri spines	4	*morii* and *sobrina*; *plumata* and *platychela*		
10. P5♂, left Re1 length	2	*morii*, *sobrina*, and *platychela*	*plumata*	
11. P5♂, right Re1 width	2	*morii*, *sobrina*, and *platychela*	*plumata*	
12. P5♂, right Re1 morphology	3	*morii* and *sobrina*	*plumata*; *platychela*	
13. P5♂, right Re 2-3 morphology	3	*plumata* and *sobrina*	*morii*; *platychela*	
14. A1 ♂ right seg. 18 length	2	*morii* and *sobrina*; *plumata* and *platychela*		
15. Spermatophore attachment	3	*morii* and *sobrina*	*plumata*; *platychela*	
16. Geographical distribution	4		*plumata*; *platychela*; *morii*; *sobrina*	
17. Latitude and depth distribution	2	*morii*, *sobrina*, and *platychela*	*plumata*	

Frequency of similarities in 17 characters:

morii and *sobrina* linked in 15 instances or 82%.
platychela linked with *morii* and *sobrina* in 4 instances or 24%.
plumata and *platychela* linked in 10 instances or 59%.
plumata and *sobrina* linked in 1 instance or 6%.
plumata unique in 7 instances or 41%.
platychela unique in 5 instances or 29%.
morii unique in 3 instances or 18%.
sobrina unique in 1 instance or 6%.

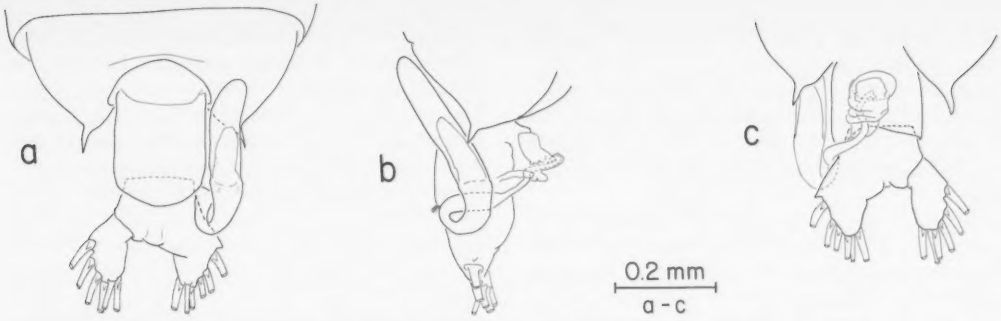

FIGURE 34.—ThIV-V and urosome of female *Pontellina sobrina* with attached spermatophore: **a.** dorsal view; **b.** lateral view; **c.** ventral view.

The program calculates an index of affinity for all possible pairs of species as the geometric mean of the proportion of common character states corrected for the number of characters used in the analysis: i.e., $J/\sqrt{A \times B} - \frac{1}{2}\sqrt{B}$, where A and B are the total number of characters recorded for the two species, $B \geq A$, and J is the number of shared character states. Values of the index above 0.5 have been found empirically to provide objective repeatable groupings of related sets of values.

A number of characters listed in Table 9 were omitted from the recurrent group analysis to avoid biasing the computations with redundant information. Characters 1, 2, and 4 were not scored since their morphometric states are determined largely by the value of character 3. Characters 11 and 14 were deleted since they parallel character 10 in showing a direct relationship to TL and to furcal length. In the absence of a fossil record the distributional characters 16 and 17 were not scored on the intuitive grounds that they are complex derivatives of both 1) overall genetic adaptation and 2) fortuitous abiotic historical events that might obscure essential phylogenetic patterns. All of the scored characters were weighted equally and disregard the preliminary results from SEM observations.

The recurrent group analysis reveals only one grouping with an index higher than 0.5, that of *morii* and *sobrina* (Table 10). Similarity between *plumata* and *platychela* falls well below the acceptable level of significance. The other possible pairings are dissimilar in most to virtually all of the 10 characters used in the analysis. Assuming equal rates of evolution the results indicate that the divergence of *plumata*, *platychela*, and the *morii-sobrina* lineage are likely to be divisions of greater age than that of *morii* and *sobrina*.

GEOGRAPHICAL VARIATION AND SYMPATRY

In the course of this study two conspicuous and parallel instances of geographical variation were encountered in the fifth legs of *plumata* females. This variation was expressed in the number of spines at the distal end of the endopod and the length of the exopod relative to that of the endopod.

As noted above the number of spines on the endopod of the female's fifth leg is polymorphic throughout *Pontellina*. The bilateral two-spined morph is overwhelmingly dominant in *morii* and *sobrina*. However, four morphs are common in *platychela* and *plumata*. Comparison of randomly selected samples of Atlantic specimens of *plumata* with specimens from the Indian and Pacific Oceans indicate significant differences

TABLE 10.—Values of the recurrent group affinity index (Fager, 1969) and the probability of obtaining this or higher values by chance for all possible pairs of *Pontellina* spp. Further discussion in text.

Species pair	Affinity index	*p*
morii and *sobrina*	0.642	<0.001
platychela and *plumata*	0.242	>.4
platychela and *morii*	0.042	>.8
platychela and *sobrina*	0.042	>.8
plumata and *sobrina*	0.042	>.8
plumata and *morii*	0	—

in the frequency of the four morphs (Table 11). The bilateral one-spined morph is much more frequent than the bilateral two-spined morph in the Atlantic Ocean whereas in the Indian and Pacific Oceans the frequencies of the two morphs are more alike and the differences are not significant.

Notably, the frequencies of the morphs in *platychela* differ significantly from those of the *plumata* sample from the Atlantic but not from those of the Indian and Pacific samples of *plumata*. Of the pairs of species sharing common boundaries only *morii* and *sobrina* do not appear to have appreciably different morph frequencies (Table 11).

In the ratio exopod to endopod length for the fifth legs in females, the distribution of the Atlantic sample of *plumata* differed significantly from those of the Indian and Pacific Oceans (Table 12). As in the case of the endopodal spines, pairs of species with common boundaries showed significantly different distributions of the exopod-endopod ratios.

Extrapolating from the similarity of Indian and Pacific Ocean samples, differences between Atlantic and Indian-Pacific populations of *plumata* appear to be geographically abrupt. Thus they may be viewed as reflecting 1) local pressures on *plumata* within each geographical population, 2) restricted gene flow between the Indian and Atlantic Ocean populations, 3) or both. *P. plumata* showed the highest frequency of unique character states in *Pontellina* (Table 9). Furthermore it tends to occupy a conspicuously peripheral position relative to the other three species in its dimensions of sexually modified appendages in both sexes (e.g., Figures 27, 28, 30, 31). It is also the only species of the genus sharing common boundaries with the other three species of *Pontellina*. Therefore, the geographical differences between Atlantic and Indian-Pacific populations of *plumata* parallel the extensive character divergence (Mayr, 1970: 51-53) otherwise distinguishing the species. Considering the fact that all morphological structures involved are sexually modified it would appear that we are witnessing reinforcement of premating barriers (Dobzhansky, 1970:376-382).

Similar disjunct morphological differences distinguishing Atlantic from Indian and Pacific populations of epipelagic calanoids have been reviewed (Fleminger and Hulsemann, 1973) and the number of examples increased (Fleminger and Hulsemann, 1973; Fleminger, 1973). Similar patterns in the strength of divergence in secondary sexual characters relative to

TABLE 11.—X^2 test of homogeneity in the distribution of spines on the endopod of the fifth legs in adult females.

	Number of spines on endopod (left leg-right leg):				
	2-2	1-2	2-1	1-1	
Population	Number of specimens				Total
platychela, Atlantic Ocean	38	16	12	34	100
plumata, Atlantic Ocean	22	11	16	51	100
plumata, Pacific Ocean	39	14	15	32	100
plumata, Indian Ocean	41	11	18	30	100
morii, Indian Ocean	94	2	1	3	100
morii, Pacific Ocean	98	0	2	0	100
sobrina, eastern tropical Pacific Ocean	99	1	0	0	100

	X^2	d.f.	p
plumata Atl. vs. *plumata* Pac.	9.48	3	$<0.025\ p\ >0.01$
plumata Atl. vs. *plumata* Ind.	11.3	3	0.01
plumata Pac. vs. *plumata* Ind.	0.76	3	$<0.9\ p\ >0.75$
platychela vs. *plumata* Atl.	9.14	3	$<0.05\ p\ >0.025$
platychela vs. *plumata* Pac.	3.61	3	$<0.5\ p\ >0.25$
platychela vs. *plumata* Ind.	2.5	3	$<0.75\ p\ >0.5$
morii Pac. vs. *sobrina*	3.01	3	$<0.5\ p\ >0.25$
morii Ind. and Pac. vs. *plumata* Ind. and Pac.	146.84	3	<0.001
sobrina vs. *plumata* Pac.	84.34	3	<0.001

TABLE 12.—Comparison by rank test (Tate and Clelland, 1957:89) of the ratio exopod length to endopod length in the fifth legs of adult females.

Samples tested	Median	Range	*N*	*T* obs.	*Z*	*p*
1. *plumata*, Atlantic Ocean	2.54:1	2.10-3.08:1	21	856.5	3.58	<0.01
plumata, Indian and Pacific Oceans	2.29:1	1.97-2.71:1	38			
2. *plumata*, Indian Ocean	2.27:1	2.01-2.71:1	9	373	0.38	0.7
plumata, Pacific Ocean	2.31:1	1.97-2.64:1	29			
3. *plumata*, Atlantic Ocean	2.54:1	2.10-3.08:1	21	967.5	2.85	<0.01
platychela, Atlantic Ocean	2.27:1	1.69-2.91:1	49			
4. *plumata*, Indian and Pacific Oceans	2.29:1	1.97-2.71:1	38	1655.5	0.14	0.88
platychela, Atlantic Ocean	2.27:1	1.69-2.91:1	49			
5. *sobrina*, eastern tropical Pacific Ocean	1.29:1	1.07-1.50:1	52	1911.5	5.58	<0.001
morii, Indian and Pacific Oceans	1.45:1	1.22-1.76:1	55			

sympatry have been discussed in recent studies on the calanoid genera *Labidocera* and *Clausocalanus* (Fleminger, 1967b, in press; Frost and Fleminger, 1968). The similarity of the *plumata* case to the character displacement found in North American chorus frogs (*Pseudacris*), reviewed by Littlejohn (1969, Figure 3), is especially noteworthy. Differing only in geographical scale, both cases support the view of a growing number of workers that premating isolating mechanisms tend to be a product of sympatry resulting from expansion of the range of daughter populations that have diverged in geographical isolation (Alexander, 1969).

REMARKS ON HABITAT BIOGEOGRAPHY

Vertical Distribution

Essentially similar results from a number of independent sets of published observations delineate general features of the vertical distribution of *Pontellina*. The genus has been found commonly between the surface and 200 m. Unfortunately differences between the congeners were not noticed, and all specimens were regarded as representing a single species. Though individuals may on occasion appear below 200 m, the largest numbers have been taken regularly between the surface and 100 m (Vinogradov, 1968). Diurnal migrations seem to be neither consistent nor extensive in vertical distance (Wilson, 1942; Heinrich, 1961; Vinogradov and Voronina, 1964; Roehr and Moore, 1965). Vinogradov and Voronina's report of a pattern of latitudinal variation in the depth range of *Pontellina* is particularly interesting in the light of differences in the latitudinal distribution of *plumata* and the equatorial species. In central waters the daytime 80% level (i.e., the depth above which 80% of the population occurs) was found at 200 m, and the highest concentrations appeared between 50 and 100 m. In equatorial waters of the eastern Pacific the daytime 80% level was found between 100 and 150 m, and the highest concentrations varied between the 0 to 25 m and the 25 to 50 m sampling strata.

Wilson's (1942) records of *Pontellina* during Cruise VII of the *Carnegie* were based on samples collected with open nets routinely deployed at 0830 h local time at three depths (0, 50, and 100 m) and towed horizontally. As in Vinogradov and Voronina's (1964) results, Wilson's data also show variation in frequency of captures and abundance at the three depths relative to the geographical origin of the samples (Table 13).

Vinogradov and Voronina (1963) and Voronina (1964) found the largest number of *Pontellina* in equatorial surface waters of the eastern Pacific Ocean. They noted that the genus tends to concentrate in upwelling regions along zones of divergence and in the vicinity of the tropical convergence.

Previous observations that the genus *Pontellina* occurs chiefly above 100 m in the more

eutrophic equatorial latitudes but may typically extend through 200 m or more in the oligotrophic subtropics must now be viewed within the complexity of three tropical and one tropical-subtropical species. In this context, vertical distribution appears to differ among the species: i.e., *plumata* probably has a deeper range than its three tropical congeners. Confirmation requires analysis of vertically stratified sampling from regions supporting *plumata* and one or more of its cognates.

Abundance

Interest in patterns of geographical distribution relative to phylogenetic affinities among the species prompted us to make preliminary comparisons of abundance among the species of *Pontellina*. For the analysis we selected sets of similarly collected, quasi-synoptic, quantitative samples that represented the epipelagic layer between 150 m or 200 m and the surface. The sets of samples comprise transects crossing the equator at different longitudes in the Pacific Ocean (Figure 1b, Table 14). Only adults were tabulated, the mesh width of the plankton nets usually being too large (~0.5 mm) to retain younger copepodids (Table 15). The hour of sampling was ignored in the absence of appreciable differences in either frequency of occurrence or mean abundance of *Pontellina* between samples collected at day or night (Tables 16, 17).

The mean abundance of species of *Pontellina* ranged from 0.01 to 0.9 per m^3 (Figure 35). Abundance in the Pacific followed a generally familiar pattern. Higher values appear in the eastern third of the Pacific as well as in the Austral-Asian seas and the Indian Ocean while lower values predominate in the middle and western Pacific (Figure 35).

The three species, *P. plumata*, *morii*, and *sobrina*, tend to vary independently in abundance. Mean abundance and frequency of occurrence values from the Indian Ocean and Austral-Asian seas are similar for *morii* and *plumata*, though evidence of finer-scale geographical differences separating the two species within the Indian Ocean have been noted (Figure 38). Eastward across the Pacific the abundance and occurrence of *plumata* persist or even increase up to but not beyond the boundary of the eastern tropical Pacific where *sobrina* predominates.

P. morii differs from *plumata* by showing a sharp decrease in abundance across the entire Pacific Ocean. However, high numbers of *morii* were found between 10 m and the surface south of the equator along long. 92°W. This is too distant for direct transport from the main area of abundance in the Indian Ocean and Austral-Asian seas; the unusually high values for *morii*, 1.96 per m^3 at lat. 4°16′S and 0.16 per m^3 at lat. 12°19′S, suggest recruitment by local reproduction.

TABLE 13.—Occurrence of *Pontellina* by sampling depths at selected stations of the Carnegie cruise VII (Wilson, 1942). Analysis limited to Carnegie stations providing abundance estimates from all three sampling depths. Grouping of the stations under a particular species or combination of species determined by its geographical origin relative to the distribution of species of *Pontellina* determined by the present study. Values are the sums of numerical equivalents of Wilson's index for *Pontellina* abundance divided by the number of stations in the geographical group. Index equivalents are: 1 = 1-5 specimens (trace); 2 = 6-10 specimens (rare); 3 = 11-24 specimens (frequent); 4 = 25-50 specimens (common); 5 = >50 specimens (abundant).

Probable dominant species	Sum of abundance / No. stations			Carnegie station numbers
	0 m	50 m	100 m	
sobrina	2.66	0.33	1.33	35, 37, 38
morii	1.83	0.0	0.50	40, 41, 43-45, 48
plumata-morii	1.05	1.11	0.83	98, 99, 101, 103-108, 151, 153-160.
plumata-platychela	1.00	1.33	0.67	22, 23, 27, 31, 32, 34
plumata	0.50	0.67	0.50	16, 18, 49-52, 56, 57, 67, 79, 94, 96, 97, 109,112,132,133,135,136,139,140,142, 145, 149

TABLE 14.—Mean abundance (No./m³) and frequency of occurrence of adult *Pontellina* in sets of samples forming meridional transects crossing the Equator. *Vertical tows with Indian Ocean Standard Net (~200-0 M). ** Oblique tows with CalCOFI Standard Net (~200-0 m or less).

Region	Longitude	Latitude	No. of Samples	Sampling dates	*plumata*		*morii*		*sobrina*		*platychela*	
					$\bar{x}$ No./m³	Percentage occurrence	$\bar{x}$ No./m³	Percentage occurrence	$\bar{x}$ No./m³	Percentage occurrence	$\bar{x}$ No./m³	Percentage occurrence
Indian Ocean	40°E-80°E	35°S-25°N	233*	Jan.-Dec. 1962-65	0.0741 ± .028	33	0.0678 ± .019	29	0	0	0	0
	80°E-110°E	27°S-18°N	107*	Jan.-Dec. 1962-64	0.0438 ± .034	48	0.0425 ± .020	37	0	0	0	0
Austral-Asian Seas	120°E-130°E	12°S-12°N	23**	Mar.-May 1961	0.0395 ± .015	83	0.0200 ± .010	65	0	0	0	0
Pacific Ocean	156°E-164°E	12°S-12°N	23**	Aug.-Sep. 1956	0.0182 ± .008	83	0.0045 ± .004	22	0	0	0	0
	174°W-160°W	06°S-21°N	15**	Aug.-Sep. 1956	0.0313 ± .030	40	0.0033 ± .005	20	0	0	0	0
	126°W	12°S-20°N	22**	Feb.-Mar. 1967	0.0710 ± .037	77	0.0034 ± .003	18	0	0	0	0
	124°W-112°W	14°S-17°N	13**	Feb. 1953	0.0938 ± .090	46	0	0	0	0	0	0
	113°W- 86°W	05°N-16°N	23**	Apr.-May 1958	0.0008 ± .0001	4	0.0004 ± .0001	4	0.0243 ± .021	43	0	0
	95°W	10°S-15°N	19**	Sep. 1967	0.0058 ± .006	21	0.0031 ± .005	11	0.0863 ± .072	79	0	0
	92°W	20°S-10°N	22**	Feb.-Mar. 1967	0.0077 ± .007	18	0.0095 ± .013	23	0.0186 ± .014	36	0	0

TABLE 15.—Above: Maximum linear dimensions of *Pontellina* cephalothorax. Dorso-ventral height taken in lateral view includes Mx2 with setal fan closed, width across trunk taken in dorsal view (mm).
Below: Mesh width of nets listed in Table 14.

Copepodite stage	II	III	IV	V		Adult	
Sex	—	—	—	♂	♀	♂	♀
Typical specimen	0.30 × 0.28	0.38 × 0.34	0.48 × 0.44	0.61 × 0.56	0.62 × 0.60	0.70 × 0.66	0.90 × 0.75
Small specimen	0.28 × 0.26	0.36 × 0.34	0.46 × 0.42	0.58 × 0.54	0.56 × 0.56	0.62 × 0.60	0.75 × 0.64

Nets[1]	Juday net	IOSN	CalCOFI SN	POFI SN
Mesh widths (mm)	0.18	0.33	0.55/0.25 (silk) 0.505/0.28 (nylon)	0.66/0.31

[1] IOSN = Indian Ocean Standard Net
CalCOFI SN = California Cooperative Oceanic Fisheries Investigations Standard Net.
POFI SN = Pacific Oceanic Fisheries Investigation Standard Net.

TABLE 16.—Comparison by Student-*t* test of mean abundance in day (0601 to 1800 h local time) and night (1801 to 0600 h local time) collections. Samples of each set selected for similarity of geographical origin, collecting procedures and the presence of the species, i.e., samples negative for the species omitted. Samples derived primarily from those listed in Table 14.

Species	Source of samples	Day mean/m³	s^2	N	Night mean/m³	s^2	N	t	p
plumata	Indian Ocean	0.0945	2.7318	70	0.1048	1.7640	48	0.0370	>0.9
	Austral-Asian Seas	0.0483	0.1488	12	0.0413	0.0784	7	0.6000	>0.9
	Pacific Ocean	0.0770	1.2224	43	0.0405	0.1720	41	0.1986	>0.8
	Atlantic Ocean	0.0857	2.7429	7	0.0133	0.0033	3	1.0251	>0.3
morii	Indian Ocean	0.1504	3.7540	56	0.1550	5.1996	41	0.0107	>0.9
	Austral-Asian Seas	0.0300	0.0400	12	0.0400	0.1040	6	0.0081	>0.9
	Pacific Ocean	0.0332	0.0804	22	0.0462	0.4721	24	0.0881	>0.9
sobrina	Pacific Ocean	0.0307	0.0858	16	0.0914	2.8169	35	0.1423	>0.8

TABLE 17.—Occurrence of *Pontellina* spp. in day (0601 to 1800 h local time) and night (1801 to 0600 h local time) samples. + present, − absent.

	Day		Night			
	+	−	+	−	X^2	p
Atlantic Ocean:						
plumata	25	16	13	22	3.389	$0.1 > p > 0.05$
platychela	23	18	23	12	0.383	$0.75 > p > 0.5$
Eastern Pacific Ocean:						
plumata	15	19	13	49	4.360	$0.05 > p > 0.025$
morii	6	28	13	49	0.015	$0.9 > p > 0.75$
sobrina	9	25	26	36	1.648	$0.25 > p > 0.1$
Indian-Western Pacific Ocean:						
plumata	108	30	87	31	0.491	$0.5 > p > 0.25$
morii	80	58	66	52	0.040	$0.9 > p > 0.75$

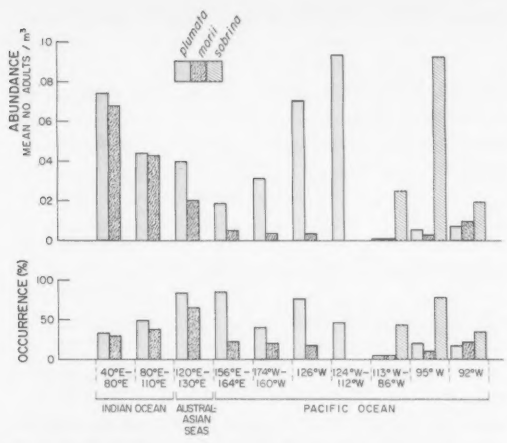

FIGURE 35.—Mean abundance (No. adults/m³) and percentage frequency of occurrence in sets of samples shown in Figures 1b and 38 and listed in Table 14. Confidence limits of the means shown in Table 14. Further discussion in text.

The appearance of *sobrina* is restricted to the eastern tropical Pacific where its abundance and occurrence resemble the values for *morii* and *plumata* in their regions of dominance, respectively.

Quantitative data on *Pontellina* in the Atlantic Ocean are few. In six quantitative samples from the western Atlantic *plumata* abundance ranged from 0.01 to 0.46 adults per m³. Two samples containing *platychela* provided estimates of 0.001 and 0.08 adults per m³.

Extremely high values of *plumata* s.l., however, have been reported from the Atlantic. Judging from their geographical origin, the northeastern Gulf of Guinea, these abundance estimates (Mahnken, Jossi, and McCabe, 1968) are probably referrable to *platychela*. Mahnken and his co-workers record the species at 18 of 63 sampled localities scattered offshore from the Bight of Benin west to Cape Palmas. They indicate areal abundance of the species by contouring selected class intervals of number per 1,000 m³ water strained. In lieu of the actual estimates per sample we used midpoints of each contoured interval to calculate the mean abundance. The yield is a surprisingly high mean of 1.01 individuals per m³, an order of magnitude higher than our highest mean values from the Pacific and Indian Oceans. Aside from possible bias introduced by our extrapolations several factors may be responsible for these unusually high values: e.g., count of immature as well as adult specimens, use of nets with smaller mesh width (0.281 mm), use of surface tows in a region relatively rich in zooplankton presumably concentrated in the very shallow layer of tropical surface water above the permanent thermocline, etc.

Summing our mean values of *plumata*, *morii*, and *sobrina* in each meridional set of samples, we find remarkably good agreement between our abundance estimates and those derived by previous studies of *plumata* s.l. in the Pacific Ocean (Table 18). We normalized the published data to conform to the units employed in the present study. Normalization was simplified by the following assumptions:

a. we assumed 100% filtration efficiency;
b. we assumed that *Pontellina* occurs only above 200 m and, in calculating volume of water strained by the net, omitted segments extending below 200 m;
c. in sets of vertically stratified tows we considered the overall estimate of abundance as if it were from a continuous tow sampling between 200 m and the surface;
d. we assumed that previous studies on *Pantellina* failed to discriminate among the different species; the published values were regarded as representing a combined estimate of the abundance of all species of the genus found in the region.

Estimates obtained from Heinrich (1968) and Vinogradov and Voronina (1963) are about one order of magnitude higher than other middle and west Pacific estimates. These higher values may be accounted for by two factors, namely that the counts include immature copepodids and that the samples were taken with nets of 0.18-mm mesh, small enough to retain *Pontellina* copepodids of stage II and possibly of stage I as well (Table 15). Sherman's (1963, 1964) counts appear to have been derived from adult specimens, partly by inference from his text and partly from the relatively wide mesh comprising most of the filtering cone in the POFI (Pacific Oceanic Fisheries Investigation) Standard Net (0.66 mm).

TABLE 18.—Mean abundance (No. /m³) of *Pontellina* spp. in meridional transects crossing the Equator.

Region	Longitude	Latitude	Source of data	$\bar{x}$ no. adults	$\bar{x}$ no. adults and juveniles	Number of samples	Sampling months	Depth, tow, net
Indian Ocean (west)	40°E-80°E	35°S-25°N	present study	0.1419	—	233	Jan.-Dec. (1962-65)	200-0 m, vert., IOSN[1]
Indian Ocean (east)	80°E-110°E	27°S-18°N	present study	0.0863	—	107	Jan.-Dec. (1962-64)	200-0 m, vert., IOSN[1]
Austral-Asian Seas	125°E-135°E	12°S-12°N	present study	0.0596	—	23	Mar.-May (1961)	150-0 m, obl., CalCOFI SN[2] (silk)
Pacific Ocean	156°E-164°E	12°S-12°N	present study	0.0230	—	23	Aug.-Sept. (1956)	150-0 m, obl., CalCOFI SN[2] (silk)
	160°E	04°S-16°30'N	Vinogradov and Voronina, 1963	—	0.1023	17	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	176°W	14°S-13°N	Vinogradov and Voronina, 1963	—	0.3790	21	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	120°E-175°W	04°S-30°N	Heinrich, 1968	—	0.1910	91	W of 160°E Jul.-Aug. (1957)	500-0 m, vert., Juday 80 cm
							E of 160°E Nov.-Feb. (1957-58)	
	168°E-155°W	20°S-20°N	Sherman, 1964	0.1379	—	59	Jan.-Apr. (1962)	Surface, POFI SN[3]
	174°W-160°W	06°S-21°N	present study	0.0346	—	15	Aug.-Sep. (1956)	150-0 m, obl., CalCOFI SN[2] (silk)
	158°W	07°S-21°N	Sherman, 1963	0.0438	—	13	June-July (1961)	Surface, POFI SN[3]
	154°W	13°S-13°N	Vinogradov and Voronina, 1963	—	0.1172	18	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	140°W	18°S-17°30'N	Vinogradov and Voronina, 1963	—	0.1600	29	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	126°W	12°S-20°N	present study	0.0744	—	22	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN[2] (nylon)
	95°W	10°S-15°N	present study	0.0952	—	19	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN[2] (nylon)
	92°W	20°S-10°N	present study	0.0358	—	22	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN[2] (nylon)

[1] IOSN = Indian Ocean Standard Net.
[2] CalCOFI SN = California Cooperative Oceanic Fisheries Investigations Standard Net.
[3] POFI SN = Pacific Oceanic Fisheries Investigation Standard Net.

Disregarding collecting and sample enumerating procedures as well as differences among the individual species, estimates of mean abundance of *Pontellina* across the Pacific (Table 18) vary from 0.023 to 0.379 with a median of 0.1 individuals per m³. For epipelagic copepods this appears to be a rather low and remarkably uniform set of values that varies within the unusually narrow range of one order of magnitude. Summing the abundance of the three species produces a notable lack of any pronounced geographical trend though the mean abundance shows moderate, irregular undulations along the equatorial belt crossing the Indian and Pacific Oceans.

Low abundance and relatively uniform dispersion throughout the geographical region occupied by each species suggests that the species of *Pontellina* are high-order predators. This impression is supported for adults at least by the exclusive presence of animal remains in their stomach and the predominance of copepod

fragments (Table 19). Though all of the species appear to be similarly predaceous within their respective epiplanktonic communities, we must conclude that appreciable differences in the abundance and occurrence of the sibling species are indicative of real changes in habitat conditions and real differences in the adaptive optima for each species.

Remarks on Geographical Distribution

This discussion hinges upon inferences drawn from the evidence presented in the preceding sections. Chief among them are the validity of the four sibling species of *Pontellina* as separate noninterbreeding populations. Based on morphological homogeneity each population appears to be closely adapted genetically to prevailing environmental conditions in the geographically limited hydrographic systems comprising its particular habitat. Except for differences between Atlantic and Indian-Pacific populations of *plumata* morphological indications are that panmixis prevails in each species.

The three tropical species, *morii*, *sobrina*, and *platychela*, occupy eutrophic waters characterized by equatorial upwelling and a shallow, steeply graded, permanent thermocline. The mixed layer overlying the thermocline is relatively homogeneous in temperature and has been referred to as Tropical Surface Waters (Wyrtki, 1966, 1967). In our use of this term, Tropical Surface Waters are restricted to the surface layer in regions where the permanent thermocline has a temperature gradient of $\geqslant 0.1°C$ per m and encompasses an overall decrease in temperature from about 24° ± 1°C at the top to about 15° ± 1°C at the bottom. These pools of warm water are subjected to seasonally repetitive changes in the strength of the equatorial Trade Winds (Wyrtki, 1966, 1967; Taft, 1971). The seasonal changes produce monsoonlike reverses in the circulation of the equatorial segment inhabited by each species. This phenomenon apparently provides a sufficiently closed hydrographic circulation to maintain breeding stocks in proximity to suitable nursery grounds and thus ensures continual success of each species.

The equatorial distributions of the tropical species of *Pontellina* are not without precedence. The tropical Atlantic has previously been characterized in faunistic terms, for example, by a number of mesopelagic fishes (Backus et al., 1970) as well as by a sergestid shrimp

TABLE 19.—List of identified particles from microscopic analysis of stomach contents in adult female *Pontellina*.

Species	Specimen number	Copepod parts	"Oncaea" parts	"Paracalanus" parts	Crustacean parts	Algal parts	Source of specimen: Ocean	Station
plumata	1	x	x				Atlantic	La Creuse 5
	2	x					Indian	Dodo VI-81
	3	x	x				Pacific	Scorpio II-146
	4	x	x				Indian	Lusiad V-45
	5	x	x				Pacific	*Jordan* 57-076
	Percentage no. with ingested particles in midgut: 71%							
platychela	1	x		x			Atlantic	*Atlantis II* 20-28
	2	x	x				Atlantic	La Creuse 5
	3	x					Atlantic	*Atlantis II* 31-40
	4				x		Atlantic	*Atlantis II* 31-54
	5		x				Atlantic	*Oregon* 1289
	Percentage no. with ingested particles in midgut: 63%							
morii	1	x	x				Pacific	Troll 30
	2	x					Pacific	TRANSPAC 98B
	3	x	x				Pacific	EQUAPAC H-31
	4	x					Indian	Lusiad V-45
	5	x					Indian	Lusiad II-14
	Percentage no. with ingested particles in midgut: 63%							
sobrina	1	x	x				Pacific	Bonacca 35
	2	x					Pacific	CalCOFI 5801: 153.50
	3	x	x				Pacific	Scot 45
	4	x	x				Pacific	*Jordan* 60-056
	5	x	x				Pacific	Bonacca 31
	Percentage no. with ingested particles in midgut: 83%							

(Judkins, 1972). Among the Atlantic Foraminifera listed by Bé and Tolderlund (1971) as tropical species only *Candeina nitida* shows a geographical distribution similar to that of *P. platychela*.

In general species characterizing the eastern tropical Pacific, unlike *sobrina*, tend to follow the coastline of the Americas from about lat. 30°N to 20°S and extend westward to long. 160° to 180°W: e.g., *Euphausia distinguenda*, (Johnson and Brinton, 1963), *Eucalanus inermis*, (Lang, 1967), *Melamphaes spinifer*, (Ebeling, 1962), *Stomias colubrinus*, (Gibbs, 1969).

These distributions are meridionally and zonally more extensive than the limited dispersion observed in *P. sobrina* and others like *Pontella danae*, *P. agassizi*, and *Pontellopsis lubbockii* (Heinrich, 1964; Fleminger, 1967b; and unpublished records). The dissimilarities probably relate to differences in depth range, the more widespread forms having access to subsurface currents flowing northward (Wooster and Jones, 1970) and southward (Wooster and Gilmartin, 1961) under the eastern boundary currents as well as westward in the tongue of low oxygen water accompanying the North Equatorial Current which is traceable to the Philippines (Reid, 1965; Wyrtki, 1966; Tsuchiya, 1968).

Distributions of epipelagic species in the equatorial Indian and Pacific Oceans resembling that of *morii* include a number of other copepods, e.g., several species of *Eucalanus*, (Fleminger and Hulsemann, 1973; Fleminger, 1973); *Clausocalanus minor*, (Frost and Fleminger, 1968); several euphausiids such as *Euphausia diomediae*, *E. paragibba*, and *Stylocheiron microphthalma*, (Brinton, 1962); and fishes such as *Scopelogadus unispinus*, (Ebeling and Weed, 1963) and *Stomias affinis*, (Gibbs, 1969) though the lattermost is also considered to inhabit the tropical Atlantic.

Although the ubiquitous *plumata* overlaps geographically with each of the tropical species, *plumata*'s overall range lies mostly in the enormous basin of oligotrophic waters spreading across the tropics and subtropics of each ocean, waters markedly different in vertical thermal structure from those of its tropical congeners. The almost mutually exclusive distributions of *plumata* and its more localized congeners, *platychela* in the equatorial Atlantic and *sobrina* in the eastern tropical Pacific, are evidence of relatively intensive environmental gradients and the adaptive response to appreciably different environmental optima, which separate the distributions of these pairs of species.

For example, *morii* has been found at the edge of the south Atlantic as well as the edge of the eastern tropical Pacific; concomitantly *sobrina* occurs in the North Equatorial Current, but successfully extends only a few degrees of longitude to the west of its habitat; *platychela* is adjacent to but fails to establish itself in the Sargasso Sea; finally *plumata*, despite apparent circumglobal distribution, does not appear in large numbers where its equatorial congeners abound. Thus, the optimum habitats appear to be regionally distributed and those that are contiguous are sufficiently different to prevent colonization by expatriated congeners transported to the margin of the habitat. The possibility of interference among the species is open but in the light of available knowledge of calanoids it seems intuitively to be most unlikely.

Thus, the two classes of epipelagic warm-water distributions found in *Pontellina* suggest a fundamental dichotomy in the circumglobal warm-water belt. The three tropical species correlate with geographically separated shallow lenses of eutrophic water. Each lens is known to overlie regions of intense temperature and oxygen gradients and to be partially bounded by the similarly intense tropical convergences (Neumann and Pierson, 1966).

P. plumata, however, correlates with the circumglobal warm-water pool that is largely oligotrophic. The oligotrophic pool tends to be deep, the permanent thermocline often exceeding 200 m in depth. Temperature gradients in the thermocline and along its margins at the subtropical convergence are relatively weak, and oxygen is generally at or near saturation (Neumann and Pierson, 1966). Evidence that the Atlantic pool may be at least partially isolated with respect to *Pontellina* whereas the Indian and Pacific pools are confluent is suggested by morphological differences in the *plumata* populations reported above.

The circulation systems and physical conditions known to maintain these lenses of eutrophic tropical water and the pools of oligotrophic tropical-subtropical waters are the obvious mechanisms sustaining the geographical dis-

tribution of the four species of *Pontellina*. This is apparent in the relationship between the distribution of each species and the location of prevailing near-surface isotherms that locate the hydrographic limits of these bodies of water. The localities for the tropical species are largely enveloped by the mean winter season position of the 24°C isotherm at 10 m (Figure 36), the lower thermal limit of Tropical Surface Water. The 10-m depth was chosen to reduce the influence of diurnal fluctuations. The localities for *plumata*, however, vary broadly between the position of the 20° and 15°C mean winter season isotherms (Figure 37). Factors confining the distributions to the observed limits, however, are not obvious; more data on depth range, vertical migratory behavior, and depth of food organisms would probably be enlightening.

Notably, more than three-quarters of the samples (77.5%) containing *Pontellina* yielded specimens of only one species. To examine joint occurrences of *Pontellina* congeners more closely, all capture records of a species were tallied by ocean and grouped with respect to the presence or absence of other congeners in the same sample (Table 20). Comparison of singular and joint occurrences for all possible pairings indicates that the latter are relatively infrequent. In no case of joint occurrences did the index of affinity (Fager and McGowan, 1963) reach a positive value. No two species within the genus would appear to occupy the same spatial habitat or, in other words, be members of the same community. Thus, the extensive overlapping of *morii* and *plumata* in the equatorial Indian and Pacific Oceans may be viewed as a function of intermingling due to the spatial proximity of the two habitats and perhaps also due to a greater number of similarities shared by these two habitats than between those of the other possible pairings within the genus.

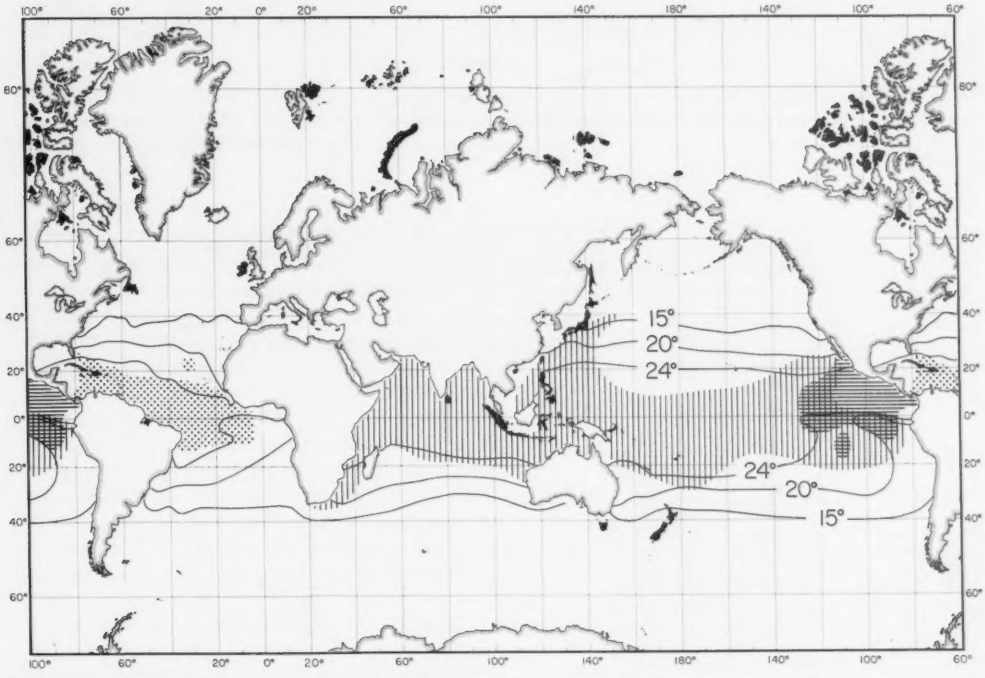

FIGURE 36.—Comparison of geographical area enveloping all capture records of tropical species of *Pontellina* with selected mean isotherms at 10 m for winter season of each hemisphere. Data from Muromtsev (1958, 1963) and Wyrtki (1971). Dotted shading outlines capture records of *P. platychela* shown in Figure 8; horizontal shading outlines capture records of *P. sobrina* shown in Figure 15; vertical shading encloses the capture records of *P. morii* shown in Figure 12.

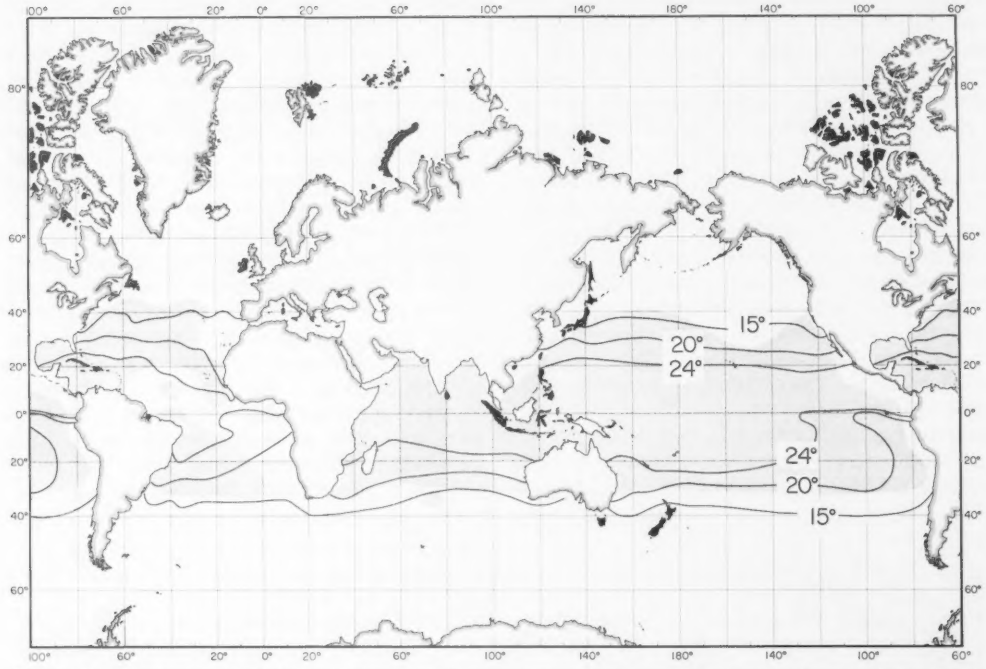

FIGURE 37.—Comparison of shaded area enveloping all capture records of *Pontellina plumata*, shown in Figure 5 with selected mean isotherms at 10 m for winter season of each hemisphere. Data from Muromtsev (1958, 1963) and Wyrtki (1971). Further discussion in text.

TABLE 20.—Separate and joint occurrences among species of *Pontellina*. Values in parentheses are the index of affinity; a value greater than 0.5 suggests joint membership in the same communal assemblage of species.

	plumata	*morii*	*sobrina*	*platychela*	Total
Indian Ocean and Australasian Seas:					
plumata	129	96 (-7.01)	0	0	225
morii		78	0	0	78
sobrina			0	0	0
platychela				0	0
Total	129	174	0	0	303
Pacific Ocean:					
plumata	136	46 (-3.77)	23 (-5.20)	0	205
morii		23	6 (-2.69)	0	29
sobrina			85	0	85
platychela				0	0
Total	136	69	114	0	319
Atlantic Ocean:					
plumata	80	0	0	14 (-3.93)	94
morii		0	0	0	0
sobrina			0	0	0
platychela				58	58
Total	80	0	0	72	152
All records combined:					
plumata	345	137	18	4	514
morii		101	1	0	102
sobrina			85	0	85
platychela				58	58
Totals	345	238	104	72	759

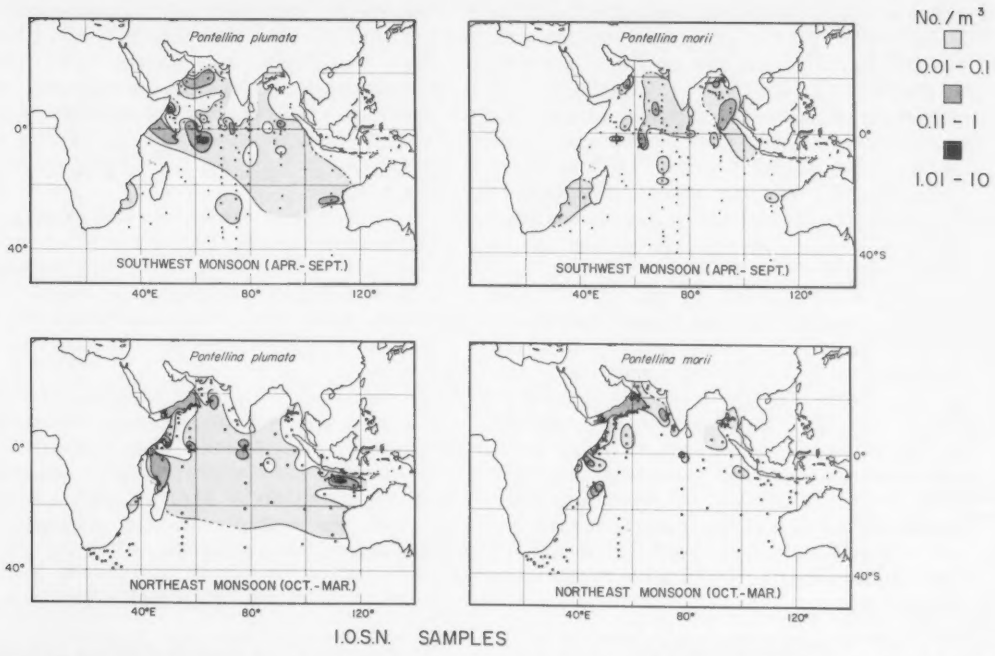

FIGURE 38.—Abundance of *Pontellina morii* and *P. plumata* in Indian Ocean Standard Net (IOSN) collections. Samples collected during southwest and northeast monsoon seasons. Dots represent localities sampled. Abundance values are estimated number of adults per m^3 water strained.

P. morii and *plumata* exhibit distinctive distributions in both monsoon seasons (Figure 38) as well as general zonal separation (Figure 39), differences that are blurred in charts prepared without regard for seasonal variation (e.g., Figures 5, 12). During the southwest monsoon, *plumata* appeared in large numbers off the Somali coast and near the Seychelles whereas *morii* was much more frequent in the eastern Arabian Sea and the eastern Bay of Bengal. In the northeast monsoon both species were abundant in the Somali Current. However, only *morii* appeared to be common in and about the Andaman Sea whereas an indication of large numbers of *plumata* appeared just south of Java.

Morphological relationships analyzed above indicate the species have common ancestry that produced three main lines of descent represented respectively by *plumata*, *platychela*, and the Indian-Pacific tropical pair of siblings, *morii* and *sobrina*. Ample evidence of co-occurrence

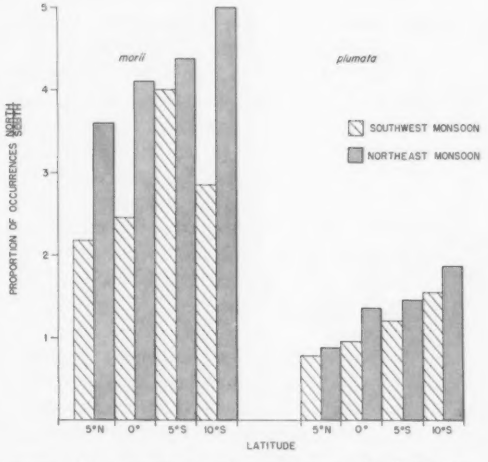

FIGURE 39.—Frequency of occurrence of *Pontellina plumata* and *P. morii* in the Indian Ocean north of selected latitudes compared to that south of the same latitudes.

without intergradation between *morii* and *sobrina* support the conclusion that both are valid species that have evolved relatively recently.

Morphological-geographical patterns provide inferential evidence that sympatry among subsets of the four species have led to modifications of secondary sexual features, presumably in the course of developing premating barriers to hybridization. Obvious examples of this emerge from comparison of pairs of species which have extensive contiguous boundaries: e.g., *plumata* and *platychela* in the Atlantic and *plumata* and *morii* in the Indian and Pacific Oceans. In each pair of species the chela on the male fifth leg in the tropical congener is broadened in contrast to the slender chela found in *plumata*. In the females of each pair the hair patches on the genital segment are either missing or reduced to one pair in the tropical species while *plumata* maintains two prominent pairs. Another source of evidence lies in the geographical variations in the female fifth legs of *plumata* which follows a pattern indicative of character displacement.

CONCLUSIONS

1. The genus *Pontellina* represented by four species is epipelagic and occupies oceanic sectors of the circumglobal warm-water belt.

2. Three of the species occur chiefly in eutrophic sectors of equatorial latitudes where the layer above the thermocline is relatively homogeneous; the distinctiveness of this layer was noted by Wyrtki who refers to it as Tropical Surface Water. One species, *platychela*, occupies the tropical Atlantic; *sobrina* is in the eastern tropical Pacific; and *morii* is found in the tropical Indian and tropical Pacific Oceans.

3. The fourth species, *plumata* s.str., occurs most frequently in oceanic, oligotrophic regions in tropical and subtropical latitudes.

4. Morphological differences among the species are subtle and restricted to secondary sexual structures.

5. The four species comprise a monophyletic complex showing three basic derivatives, *plumata*, *platychela*, and a third that underwent a subsequent episode of speciation to produce *morii* and *sobrina*.

6. The female fifth leg is polymorphic and represented by four phenotypes or morphs. Geographical variation in the frequency of morphs in *plumata* distinguishes Atlantic from Indian and Pacific populations; relationships with *platychela* in the Atlantic and *morii* and *sobrina* elsewhere suggest the variation is the result of character displacement. Three of the four morphs in *morii* and *sobrina* appear to be extremely rare.

7. Each species exhibits a distinctive geographic range independent of the other three. Absence of conspicuous geographical variation indicates sufficient transport and advection to maintain panmixis within each species except the Atlantic and Indian-Pacific populations of *plumata*.

8. Abundance of all four species is low despite relatively frequent occurrence within the limits of the distribution. These indications of high-order predation are supported by examination of gut contents in sexually mature adults in which the remains consisted primarily of particles from small copepods.

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STOCK COMPOSITION, GROWTH, MORTALITY, AND AVAILABILITY OF PACIFIC SAURY, *COLOLABIS SAIRA*, OF THE NORTHEASTERN PACIFIC OCEAN

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ABSTRACT

Recent international interest in the Pacific saury *(Cololabis saira)* resource of the northeastern Pacific Ocean prompted studies to determine the stock's composition, structure, growth, mortality, and availability.

During August-September 1969-71, data were obtained from more than 5,000 fish sampled from 19 individual schools captured between southern California and Vancouver Island, B.C. Length and age frequency distributions indicate fish grow to 340 mm in length during their 6-year lifespan. Larger fish apparently migrate farthest north and consequently age at full recruitment off Washington is III or IV, and II off Oregon. Spawning is extended over most of the year and the stock is believed homogeneous. First maturity appears to be reached during the second year. Numbers of males and females were nearly equal until age IV when females began to predominate. Length-weight regressions are presented by sex. Bertalanffy growth parameters were calculated: $K = 0.42$, $L_\infty = 342$ mm, and $t_0 = -0.72$ years. The total instantaneous mortality coefficient was estimated at 1.25-2.20.

Data on distribution and availability suggest a viable domestic fishery on this species is unlikely.

In 1969, an investigation of the distribution, availability, and biology of Pacific saury, *Cololabis saira*, in the northeastern Pacific Ocean was begun by our laboratory. This study was a direct result of a tenfold decrease in combined Japanese and Soviet landings of the species in the northwestern Pacific Ocean since 1958. Unusually high market demand created international interest in the unexploited stock in the eatern Pacific Ocean.

Initial studies were concerned primarily with the development of sampling and harvesting gears (Ellis and Hughes, 1971). This paper contains results of research on the biology and availability of saury, except for parasite studies which were treated separately (Hughes, 1973). The purpose of the paper is to provide initial information on stock composition, growth, and mortality and to supplement previous studies of distribution and abundance. Data were obtained during research vessel surveys, conducted primarily during August and September 1969 off the California coast, and during August and September 1970 and 1971 off the Washington and Oregon coasts.

STATUS OF KNOWLEDGE

Parin (1960) reported that the Pacific saury inhabits the northern Pacific pelagic zone and has a continuous range from Asia to North America. Sokolovskii (1969) inferred from studies of parasites and biological and morphometric characteristics of the species that there exist within its total range, stocks distinguishable from one another—western (Asian), central (Aleutian), and eastern (American)—that there is no clear boundary between these stocks, and that there are rather wide zones of mixture of the stocks. The eastern stock ranges from Baja California to the Gulf of Alaska (Ahlstrom and Casey, 1956; Clemens and Wilby, 1961). Novikov and Kulikov (1966) found that in the eastern Pacific Ocean, saury occupied an extensive coastal region 50-70 miles wide between lat. 41° and 48°N during August-October, but that major concentrations were irregularly distributed. Their survey indicated the most dense aggregations occurred off southern Oregon during August, October,

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and November in water temperatures of 12.5 to 13.5°C. Data obtained from night-light station observations off California indicated that in the California Cooperative Oceanic Fisheries Investigations area saury occurred most frequently in waters north of San Francisco in a band 40-120 miles offshore (Smith, Ahlstrom, and Casey, 1970). Peak availability occurred during November. Results of egg surveys suggested peak spawning activity occurs off California during April, May, and June and that the standing stock in the eastern North Pacific Ocean was at least 450,000 to 500,000 tons (Ahlstrom, 1968; Smith et al., 1970).

METHODS

The method of finding schools of Pacific saury was similar to procedures employed by commercial Japanese saury vessels. The Japanese technique has been reviewed by Inoue and Hughes (1971). The Japanese use artificial lights during hours of darkness to visually locate schools near the surface and to attract the fish alongside the vessel for eventual capture. Sonar was also used to assist in detecting concentrations during 1970 and 1971. Our surveys were generally restricted to areas where surface water temperatures were between 13° and 17°C. Typically, they were conducted along a zig-zag track designed to cross boundaries between warm and cold water masses. Once detected and concentrated under the vessel's alluring lights, the total weight of each school was derived by estimating the percentage of the school captured, weighing our catch, and then computing the weight of the remaining fish.

During 1969, surveying was confined to waters off California and fishing was conducted with a Japanese-style boke-ami (Andreev, 1962). Operations were conducted off the Washington and Oregon coasts in 1970 and extended to include waters off Vancouver Island, B.C., during 1971. During those periods fishing was conducted with a small purse seine designed for capturing saury (Ellis and Hughes, 1971).

Table 1 summarizes times and locations where fishing was conducted and samples retained for biological studies. Catches were randomly subsampled aboard ship. All samples collected were returned to the laboratory for processing. Samples taken in 1969 were iced, whereas those collected in 1970 and 1971 were frozen. Only length frequency data were taken from the 1969 samples. Biological data from individual fish obtained during 1970 and 1971 included knob length[2] measured to the nearest millimeter, body weight to the nearest gram, sex, and maturity. Scales were removed for later examination.

TABLE 1.—Fishing areas and number of Pacific saury collected, 1969-1971.

Date	Coastal area	Location		Sample size
		W Long	N Lat	
Aug 1969	Calif.	124°03′	37°49′	220
Aug 1969	Calif.	124°03′	37°51′	222
Aug 1969	Calif.	124°03′	37°53′	143
Aug 1969	Calif.	123°59′	37°55′	52
Aug 1969	Calif.	123°48′	37°58′	31
Sept 1969	Calif.	122°23′	36°10′	160
Sept 1970	Oreg.	125°50′	45°03′	299
Sept 1970	Oreg.	125°11′	44°33′	300
Sept 1970	Oreg.	125°08′	44°30′	300
Sept 1970	Wash.	126°02′	47°43′	284
Sept 1970	Wash.	125°58′	47°41′	192
Sept 1970	Wash.	126°00′	47°39′	191
*July 1971	Calif.	120°00′	33°00′	98
Aug 1971	Van. Isl.	127°06′	49°16′	105
Aug 1971	Wash.	126°04′	48°21′	512
Sept 1971	Oreg.	125°01′	44°01′	506
Sept 1971	Oreg.	124°59′	43°55′	508
Sept 1971	Oreg.	125°00′	43°54′	508
Sept 1971	Oreg.	125°02′	44°02′	268
Sept 1971	Oreg.	125°04′	43°58′	419
			Total	5,248

* Sample captured with variable mesh gillnet. This sample used only in the growth analysis.

Sex determination of fish measuring less than 230 mm was generally difficult. When gross examination of gonads proved inadequate, samples were further subsampled—the gonads cross-sectioned and examined for the presence of a lumen under 10× binocular microscopes.

Age was determined from plastic impressions of scales (Clutter and Whitesel, 1956) examined with a microprojector device (Mosher, 1950). Age determination of Pacific saury has long been a point of contention between Soviet and Japanese scientists working in the western Pacific (Kotova, 1958; Hotta, 1960). Details of assessment criteria by which ages were determined for this report have been documented by Mosher.[3]

[2] Knob length (Kimura, 1956)—the distance between the tip of the lower jaw and the posterior end of the muscular knob on the caudal base—has been accepted internationally as the unit of length measurement for saury.

[3] K. H. Mosher. Age determination of eastern Pacific saury using scales. Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash. Unpubl. manuscr.

Preliminary scale studies indicated that the samples might be of two races of fish with different growth patterns—those with a wide zone of initial growth (distance between the focus and first annulus) and those with a much narrower zone of initial growth. Similar growth patterns have been detected by Japanese scientists on scales of fish of the western stock of Pacific saury and interpreted as distinct spring- and autumn-born "subpopulations" (Hotta, 1960). Accordingly, fish were classified as being either spring-born, autumn-born, or intermediate type by examining the initial growth zone of the scale. Length-weight regressions and von Bertalanffy growth in length parameters were determined for fish of the spring- and autumn-born scale types and compared statistically. In addition, electrophoretic techniques (Utter, Hodgins, and Johnson, 1972) were employed to test for significant inter-area heterogeneity as well as heterogeneity of fish with spring- and autumn-born scale features.

STOCK COMPOSITION

Temporal and spacial variations in length, age, sex, and maturity are treated in this section. In analyzing the sex ratio and age frequency data, fish of the spring- and autumn-born scale types were treated separately.

Size and Age Composition

There was a trend toward increasing length and average age with increasing latitude. Mean lengths in the California, Oregon, and Washington-Vancouver Island areas were 201 mm, 238 mm, and 277 mm, respectively (Figure 1). Length frequency histograms (Figure 2) show there was an absence of fish <160 mm off Washington-Vancouver Island which were represented off Oregon and relatively abundant off California. Conversely, fish >300 mm were absent off California, represented off Oregon, and relatively abundant off Washington-Vancouver Island.

Samples taken off California exhibited an unusual quadra-modal length-frequency distribution believed to be a sampling artifact rather than fluctuation in year-class strength. [Three of six schools sampled were schooled by size (Figure 1) which produced the minimum length mode at 165 mm and the maximum length mode at 270 mm.]

More symmetrical length distributions were produced from the three schools sampled in 1970 and five schools sampled in 1971 off Oregon. Lengths ranged from 159 mm to 293 mm in 1970 and 158 to 330 mm in 1971. Length distributions for both years are similar, being moderately skewed to the right with a mode at 210 mm in 1970 and 235 mm in 1971.

The three schools sampled off Washington in 1970 and two schools off Washington-Vancouver Island in 1971 showed more variation between years than the Oregon samples. A bimodal distribution was more apparent in 1971, modes at 245 and 305 mm, than the moderately asymmetrical distribution in 1970 with mode at 260 mm. Lengths ranged from 160 to 334 mm in 1970, and 161 to 340 mm in 1971. The upper limit of this latter range may exceed the previously known maximum length of the species in the eastern North Pacific Ocean. Clemens and Wilby (1961) reported lengths to 14 inches (356 mm); however, it is unclear whether this is standard or total length. The two saury measuring 340 mm knob length were ripe females measuring 363 and 364 mm in total length and weighing 180 and 190 grams respectively.

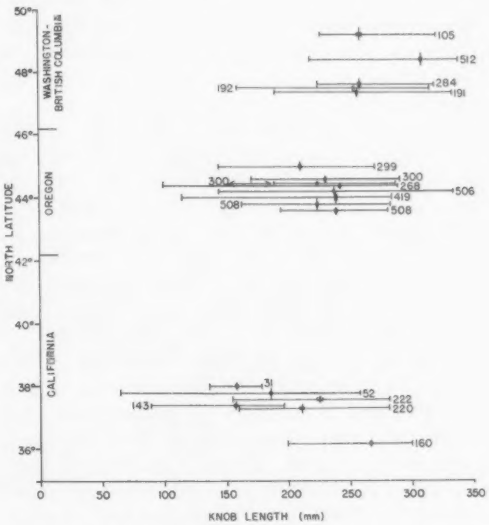

FIGURE 1.—Lengths (mean, range and S.D. of mean) of eastern Pacific saury plotted against latitude of capture. Numbers indicate sample size per school.

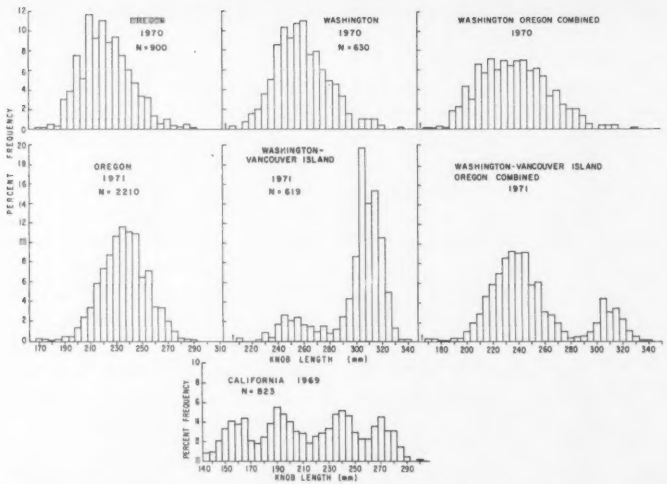

FIGURE 2.—Length frequency distributions of eastern Pacific saury captured off the Pacific coast of North America during August-September 1970-71.

Figure 2 also shows length-frequency distributions for combined Washington-Oregon samples in 1970 and Washington-Vancouver Island samples in 1971. A bimodal distribution is not apparent in 1970 but is distinct in 1971. Little variation in modes is noted between years.

Age frequency was determined from the 13 saury schools sampled off the Oregon-Washington-Vancouver Island coasts during 1970-71. Figure 3 histograms indicate the percentage of age groups by area, year, and areas combined within year.

Variations in age composition by latitude followed the expected trend established by size composition. Oregon fish were predominantly 1- and 2-year-olds while Washington-Vancouver Island fish were predominantly 2-, 3-, 4-, and 5-year-olds. Age composition of Oregon samples indicated little variation between 1970 and 1971 with age groups 1 and 2 representing 89% of the 1970 fish and 92% of the 1971 fish. In contrast, Washington fish showed considerable variation between years. In 1970, 93% of the fish were 2- and 3-year-olds while 54% were 4-year-olds in 1971. Sampling deficiencies probably account for the decline in the relative abundance of the 1968 year class between 1970 (2-year-old fish) and 1971 (3-year-olds). Fish aged as 6-year-olds were represented in 1970 and 1971 Washington samples, but it appears few fish survive beyond the age of 5.

Fish of the spring-born scale type consistently dominated all schools sampled (Figure 4) and also dominated most age groups. The greatest variation occurred at Oregon latitudes where fish of the autumn-born scale type comprised 27% of the 1970 samples and 12% in 1971. Washington samples were comprised of 21% autumn-born type in 1970 and 22% in 1971.

Sex Ratio and Maturity

The sex ratio was examined by age group for variation between area, year, and scale type.

Area differences in age composition and difficulties in determining sex of young fish hampered some comparisons; however, numbers of males and females were about equal through age 3 with females becoming predominant at age 4 and beyond. For more meaningful analysis, ages 1-3 and 4-6 were pooled for each area-year category. The sex ratio of saury of autumn- and spring-born scale types were next examined and found so similar that statistical treatment was unnecessary. Sex ratios of area-year-age group categories are presented in Table 2. While the sex ratio was age-dependent, sex composition differences in 1-3 year-olds of Washington vs Oregon catches in both 1970 and 1971 and 4-6 year-olds of Washington vs Oregon catches in 1971 were nonsignificant (0.05 level).

Size and age at first maturity could not be

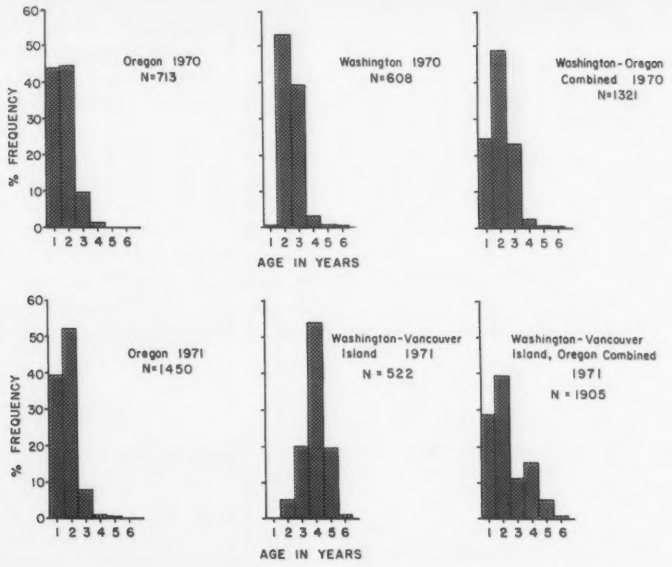

FIGURE 3.—Age frequency distributions of eastern Pacific saury captured off the Pacific coast of North American during August-September 1970-71.

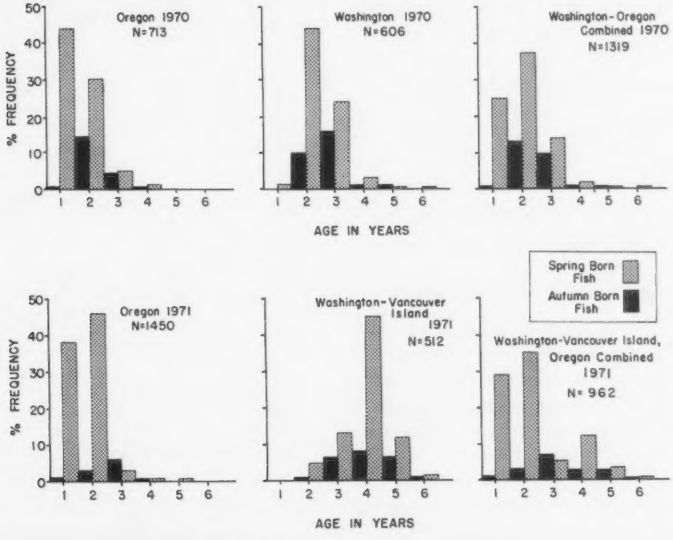

FIGURE 4.—Age frequency distributions of eastern Pacific saury showing age groups separated into spring- and autumn-born fish.

TABLE 2.—Sex ratios of age groups sampled in areas off the Pacific coast, 1970-1971.

Year-area category	Age group	Total no. fish examined	No. fish used for sex ratio	Sex ratio (% males)
1970				
Wash.	1-3	578	253	49.4
Oreg.	1-3	702	143	43.4
Wash.	4-6	28	26	30.8
Oreg.	4-6	10	10	0.0
1971				
Wash.-B.C.	1-3	179	100	54.0
Oreg.	1-3	1,365	1,024	56.1
Wash.-B.C.	4-6	391	388	37.6
Oreg.	4-6	8	6	33.3

directly determined from my samples since all but the very large fish were sexually inactive or immature upon collection. However, egg measurements obtained for ten 300-330 mm females collected off Washington in 1971 showed there were three distinct size groups of eggs: 0.1—0.4 mm, 0.8—1.5 mm, and the mature mode of 1.7—2.0 mm. Eleven smaller specimens collected off California by MacGregor[4] in March 1951 and 1954 ranged from 196 to 204 mm and contained eggs with a similar range (0.84—1.9 mm) indicating that saury are capable of reaching first maturity at lengths near 200 mm. Such fish would probably range from 1.1 to 1.4 yrs. old (Table 3).

Eighteen of the 19 schools sampled were composed principally of apparently mature fish in a resting state. The remaining school was predominantly 4-year-olds with females outnumbering males 1 to 0.73, and 96% of these were in spawning condition. Fish displaying both spring-born and fall-born growth patterns of scales were found in this school.

LENGTH-WEIGHT RELATION

The length-weight relation of saury captured in 1970 and 1971 was determined by fitting the logarithmic form of the equation $W = qL^d$, where W is weight in grams and L is knob length in millimeters, to mean emperical weights in each 5-mm length interval.

Separate relationships were determined for each hypothesized race and area-year category by sex. Using an analysis of covariance (Dixon and Massey, 1969), no significant difference in the L-W relation was detected between years, areas, or scale type, but there was a significant difference (0.05 level) between males and females.

A total of 1,170 males and 1,642 females representing immature, mature resting, and ripe saury were included in the length-weight regressions presented in Figure 5. The equation for males was $W = 3.293 \times 10^{-6} L^{3.050}$ and for females $W = 2.077 \times 10^{-6} L^{3.132}$. Females were slightly lighter than males at lengths <225 mm and heavier than males at lengths >280 mm.

GROWTH

Interpretation of growth was complicated because of the possible racial aspect and extended spawning season. Growth was determined for sexes combined because of the high probability of error in determining the sex of young fish. It was assumed that growth in length is asymptotic and that the von Bertalanffy (1938) growth equation adequately represents such growth.

Following methods of Stevens (1951), average lengths (observed and calculated from weight at age) were fitted to the equation $lt = L_\infty [1 - e^{-K(t-t_0)}]$.

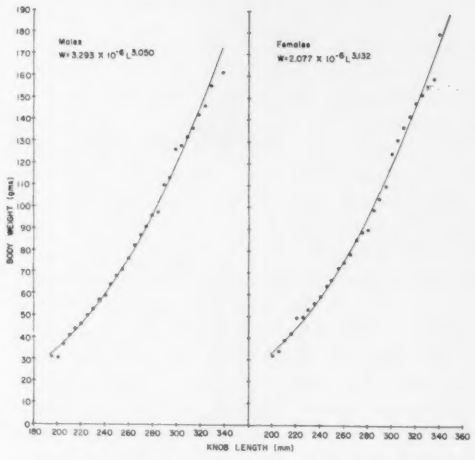

FIGURE 5.—Length-weight relation of male and female saury. The curve is fitted to mean-observed weight per 5-mm length interval.

[4] J. MacGregor, Fishery Biologist, Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Southwest Fish. Center, La Jolla, Calif., personal commun.

TABLE 3.—Average observed length at age, lengths calculated from weight at age and estimated von Bertalanffy growth parameters of hypothesized spring- and autumn-born fish.

Spring born fish			Autumn born fish		
Age (years)	Average observed length at age (mm)	Length calculated from weight at age [1] (mm)	Age (years)	Average observed length at age (mm)	Length calculated from weight at age [2] (mm)
1.10	183.9	182.5	0.75	142.8	151.2
1.40	219.0	223.6	1.00	178.7	182.1
2.40	245.5	249.3	2.00	232.1	235.8
3.40	268.8	272.7	3.00	256.8	260.6
4.40	308.6	312.5	4.00	297.0	303.0
5.40	319.8	321.4	5.00	314.5	316.8
6.40	319.9	323.0			
	$L_\infty = 351.43$	$L_\infty = 360.23$		$L_\infty = 353.45$	$L_\infty = 348.50$
	$K = 0.34$	$K = 0.36$		$K = 0.38$	$K = 0.38$
	$t_0 = -1.19$	$t_0 = -0.83$		$t_0 = -0.72$	$t_0 = -1.02$

1 $W = 1.497 \times 10^{-6} L^{3.189}$
2 $W = 1.809 \times 10^{-6} L^{3.155}$

Growth was first compared between fish of the autumn- and spring-born scale type. Table 3 summarizes the respective sets of length at age data and presents growth parameters. Little difference is noted between respective sets of length at age data for the two groups of fish. Although there is no consistent advantage in using lengths derived from weights at age, it should be noted that estimated t_0 values are sensitive to the method chosen. Regardless of method, no significant differences in growth parameters L_∞ and e^{-K} existed between fish of spring- and autumn-born scale types. Their graphic similarity is shown in Figure 6 where observed lengths at age and fitted curves are presented. Lack of significant differences in growth patterns between fish of spring- and autumn-born type suggested that respective data sets be pooled and that a single growth curve be presented (Figure 7). The resulting estimated parameters were $L_\infty = 342.36$, $K = 0.41$, and $t_0 = -0.72$. The calculated L_∞ is close to the maximum observed length of 340 mm. The estimated age at 95% growth completion was 6.5 years.

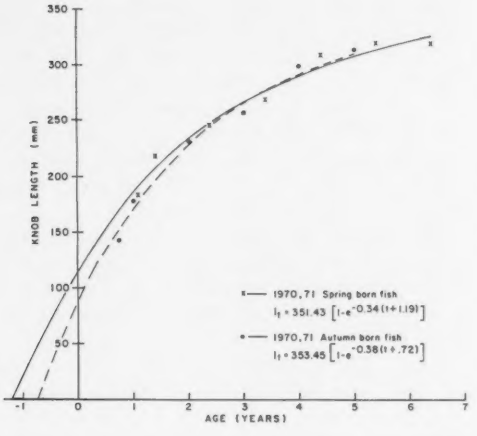

FIGURE 6.—Average observed length at age and fitted growth curves of spring- and autumn-born saury captured in offshore waters from southern California north to Vancouver, British Columbia 1970-71.

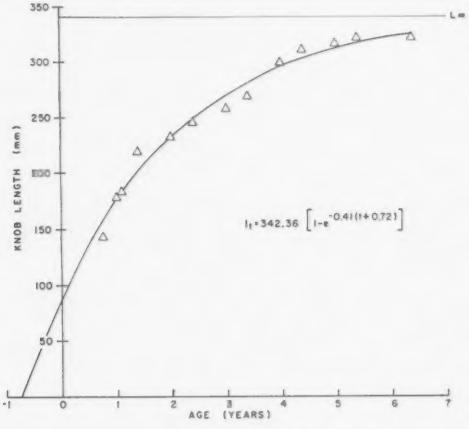

FIGURE 7.—Average observed length at age and fitted growth curve of eastern Pacific saury after pooling data from spring- and autumn-born fish.

MORTALITY

There are several limitations to the data used for estimating natural mortality: (1) Sampling was conducted during a period of apparent migration which caused the stock along the Pacific coast to become stratified in size and age composition, (2) sampling was limited and not conducted throughout the stock's entire geographical range, and (3) age frequency data indicate possible variations in annual recruitment and/or survival rate. Thus, one or more basic assumptions underlying traditional mortality models are violated to some degree. Realizing the above limitations and considering this an initial study of the adult stock, I have generated a range of estimates using several independent techniques.

A catch curve analysis (Robson and Chapman, 1961) was applied to the 1970 data since equal sampling occurred off Washington and Oregon, the only areas sampled, during that period.

Age	Coded age	No. of fish in catch
II	0	$N_0 = 644$
III	1	$N_1 = 313$
IV	2	$N_2 = 32$
V	3	$N_3 = 7$
VI	4	$N_4 = 1$
		$n = 997$

Annual survival rate estimate:

$$\hat{S} = .2876$$
$$\text{Var}(s) = 0.00017$$
$$\text{SE}(s) = 0.013$$
$$95\%\ \text{CI}(s) = .2876 + 2(0.013)$$
$$= (.2616, .3136)$$

When the above data were converted to a total annual instantaneous mortality rate, $Z = 1.25$ and 95% CI, $Z = (1.16, 1.34)$.

The raw age data were also converted to natural log form and treated by simple linear regression. The result was a significant linear relationship with $Z = 1.67$ and 95% CI, $Z = (1.41, 1.93)$.

Beverton and Holt's (1956) formula using length frequency data was also applied to the 1970 data. While this technique was designed primarily for exploited populations, its use generated another independent estimate and enabled the use of substantial numbers of fish which could not be aged.

The Beverton and Holt formula $Z = \frac{K(L_\infty - L)}{(L - L_r)}$ where L is the average length of the fish in the catch that are as large as, or larger than, the first fully recruited length L_r, estimated $Z = 1.41$ when $L_\infty = 342$ mm, $K = 0.41$, $L = 248$ mm, and $L_r = 220$ mm.

Survival rates were generated for each of the four area-year categories by subjecting respective sets of age frequency data to Jackson's (1939) technique:

$$S = \frac{N_2 + N_3 + \cdots + N_r}{N_1 + N_2 + \cdots + N_r - 1}.$$

The analysis yielded the following estimates:

Oregon, 1970; $Z = 1.58$,
Oregon, 1971; $Z = 1.80$,
Washington, 1970; $Z = 2.20$,
Washington-Vancouver Island, 1971; $Z = 1.27$.

The seven individual estimates obtained indicate a possible range of Z from 1.25 to 2.20 and an overall average Z of 1.60.

AVAILABILITY OF FISHABLE CONCENTRATIONS

Fishable concentrations of saury (>¾ ton) were usually located in waters of 15°-17°C near areas of upwelling. Surface temperatures strongly influence distribution and migration patterns of western Pacific saury (Fukushima, 1956 and 1962) as they appear to in the eastern Pacific (Ellis and Hughes, 1971). All studies indicate sharp thermal fronts affect and often dictate patterns of migration and areas where temporary concentrations may form.

Throughout the surveys, high density areas capable of sustaining productive fishing operations were rarely encountered. Most encounters were single schools (1-3 tons) or loose aggregations of fish dispersed over large areas of surface waters. The average probability of locating at least one fishable concentration during a night's operation (averaging 8 hr of searching effort and 70 miles of tracklines) was about 0.3. The relative densities decreased slightly with increasing latitudes, but large saury, which are currently in greatest commercial demand, were

more available in the northern portion of the study area.

Low availability has evidently hampered Japanese attempts to establish new fishing grounds in the eastern Pacific. Operations by about 15 Japanese saury vessels in 1970 and 19 vessels in 1971 met financial failure. Consequently, major fishery firms such as Nihon Suisan, Hoko Suisan, and Nichiro have reportedly abandoned attempts to exploit the eastern Pacific saury resource.[5]

DISCUSSION

It seems pertinent to propose some general hypotheses about the life history of the eastern Pacific saury based on information presented here and in papers by Ahlstrom and Casey (1956), Ahlstrom (1968), and Smith et al. (1970).

The coastal stratification of saury by size and age composition during at least August-September is probably due to a northerly migration by many adults from California waters. Sea surface temperatures and position of warm-cold fronts strongly influence migration patterns and rates of movement of saury in the western North Pacific Ocean (Fukushima, 1956, 1962). Several factors indicate a similar situation exists in the eastern Pacific Ocean. Our surveys indicated eastern Pacific saury display narrow limits of thermal preference and are found most often near areas of upwelling. Furthermore, there is an excellent correlation between the apparent spacial and temporal distribution of saury and average month-by-month sea-surface temperature data. Using Johnson's (1961) 12-year monthly means and a thermal preference range of 14.0° to 17.0°C, it is apparent that large quantities of saury would not begin a northerly migration from California waters before June. Migration into northern Oregon and Washington waters would not be expected to occur before July. Rapid warming during July and August produces a favorable temperature regime along the coasts of Washington, Vancouver Island, and into Queen Charlotte Sound. While temperature conditions remain favorable in September, seasonal cooling occurs off Vancouver Island and Washington during October and continues through Oregon and northern California waters in November. Thus, it appears that in addition to influencing the time and patterns of saury migration, temperature conditions could also restrict the bulk of the stock to oceanic areas between Baja California and Queen Charlotte Sound or the southern Gulf of Alaska.

From the data presented, the degree of migration appears to be dependent on size and age of fish, and many young adults and juveniles apparently remain in California waters throughout the year.

Fish exceeding 300 mm in length (primarily ages 4, 5, and 6) reach maturity during the migration in August and release their mature mode of eggs (1.8-2.0 mm) in late August or September. Since Hatanaka's (1956) work on maturity in the western North Pacific Ocean (three modes of eggs, 0.6, 1.1, and 1.9 mm) is in close agreement with this study, it seems reasonable that eastern Pacific saury release modes of eggs at about the same intervals—2 months between the first and middle mode. Thus, the second spawning of large fish would probably take place in October or November and the third spawning during the winter while off California. Younger adults, sexually inactive during August-September, probably mature and spawn during the following winter and spring while in more southerly waters, primarily off California. It is not known whether 2- and 3-year-old fish spawn more than one mode of eggs per year.

The above hypothesis would account for the reported low abundance of eggs in California waters during August-September (Smith et al., 1970) when most spawning saury occupy a northerly regime. The spawning of younger age groups coincides with peak egg abundance in California during April, May, and June. Such an extended spawning season would account for spring-born, autumn-born, and some intermediate growth patterns detected from scale samples, as well as the fact that three-quarters of the samples displayed the spring-born growth characteristic.

There seems to be little likelihood that spring- and fall-born fish constitute different races, since both types were observed spawning together in the same school. Furthermore, statistical comparisons of length-weight and

[5] J. H. Shohara (Compiler). 1972. 12 Japanese vessels licensed for distant-water saury fishing [Excerpted from Shin Suisan Shimbun Sokuho, July 18 and July 29, 1972]. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Foreign Fish. Inf. Release 72-27, p. 3. (Processed.)

growth parameters failed to disclose any significant differences between these groups. These results are in line with unpublished results of Utter whose biochemical gene frequency studies gave no indication of heterogeneity between spring-born and fall-born saury.[6] Biochemical techniques also indicated intra-area homogeneity of fish in waters between southern California and Vancouver Island. Additional samples would have been desirable for a more complete racial study; however, results of this initial study strongly suggest the eastern Pacific saury stock is basically represented by a single gene pool.

Growth, maturity, and mortality studies indicate that saury (1) display rapid growth during the first year of life, (2) are capable of attaining maturity during the second year, and (3) probably do not survive beyond 6 years of age. Results indicate the total mortality coefficient (Z) is between 1.25 and 2.20. Since fishing mortality has remained insignificant, Z would be a result of natural mortality (M), assuming migration during the sampling period has not significantly confounded the situation. Intuitively, it seems Z is a reasonable approximation of M since sampling was conducted over a wide geographical area during the middle of the migratory period. No previous estimates of natural mortality have been published for the eastern Pacific saury stock; however, Novikov (1969) reports natural mortality in the western Pacific to be about 50%. Converting to instantaneous mortality for direct comparison, his estimate would be about 0.70.

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HEAVY METALS IN THE NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, AND HARBOR SEAL, *PHOCA VITULINA RICHARDI*

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ABSTRACT

Samples of liver, muscle, and kidney from fur seal, *Callorhinus ursinus*, and liver from harbor seal, *Phoca vitulina richardi*, were analyzed for total mercury. Liver and kidney of fur seals were analyzed for lead, cadmium, and arsenic. Fur seals were from the Pribilof Islands, Alaska, and from off the Washington coast. Harbor seals were from the waters of southern California, Oregon, Washington, and the Bering Sea. All of the samples, including a fetus taken 3 mo before birth, contained mercury, lead, and cadmium. Arsenic was not detected. Mercury was highest in liver, followed by kidney, then muscle. The maximum concentration of mercury in liver was about 700 ppm in a southern California harbor seal and 170 ppm in a fur seal taken off the Washington coast. Concentrations of cadmium and lead were highest in the kidney (maximums of 1.8 ppm lead and 15.6 ppm cadmium) of fur seals. Concentrations of mercury did not correlate with age in muscle or kidney ($P > 0.05$) but did correlate significantly with age in liver ($P < 0.01$). Concentrations of cadmium and lead in liver and kidney did not correlate with age ($P > 0.05$). In samples of liver collected from harbor seals, the highest concentrations of mercury were from southern California seals.

Heavy metals are persistent contaminants that ultimately end up in the oceans. Little is known of the sublethal effects of these contaminants on living marine resources, but some heavy metals are known to be harmful. One ppb (part per billion) of four commonly used organomercurial fungicides reduced the photosynthetic rate of a marine diatom (Harriss, White, and MacFarlane, 1970). Skerfving, Hansson, and Lindsten (1970) reported chromosome breakage in humans who ate fish containing 1-7 ppm (parts per million) methylmercury.

Heavy metals are added to the sea by land erosion, volcanic activity, and man. A committee of experts selected mercury, lead, cadmium, and arsenic as the four inorganic pollutants most threatening to the marine environment (Food and Agriculture Organization of the United Nations, 1971). The same elements were selected for this study. Average levels of the four most critical heavy metals in the ocean are about 0.00003 ppm (mg/l) mercury, 0.08 ppm cadmium, 0.00003 ppm lead, and 0.003 ppm arsenic (U.S. Senate, 1970). Williams and Weiss (1973) found 0.00027 ppm mercury at 10-m depth and 0.000029-0.000096 ppm from 100- to 4,080-m depth in water samples taken 430 km southeast of San Diego, Calif.

Amounts of contaminants in seals provide us with data at this time in a marine species near the top of the food web in the ocean. Up to 172 ppm mercury in liver of northern fur seals, *Callorhinus ursinus* (Anas, 1970a); 66 ppm in liver of gray seals, *Halichoerus grypus* (Jones, Jones, and Stewart, 1972); and 24 ppm mercury in liver of short-finned pilot whales, *Globicephala scammoni* (Hall, Gilmartin, and Mattsson, 1971) have been reported. Buhler[2] reported 60 ppm cadmium in the kidney, 6 ppm cadmium in the liver, and 225 ppm mercury in the liver of California sea lions, *Zalophus californianus*. This report documents the amounts of mercury, lead, cadmium, and arsenic in northern fur seals and of mercury in harbor seals, *Phoca vitulina richardi*.

Northern fur seals are a migratory species that breed each summer mainly on the Pribilof Islands, Alaska, and on the Commander Islands

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and Robben Island, USSR. Small breeding colonies are found in the Kurile Islands, Japan, and on San Miguel Island, Calif. During winter and spring, fur seals are pelagic and migrate as far south as southern California and Japan. Fur seals feed principally on fishes and squids in offshore areas.

Harbor seals are a nonmigratory species found in the northern hemisphere in both the Pacific and Atlantic Oceans. Those collected for this study (subspecies *richardi*) are found from Mexico to the Bering Sea. Harbor seals feed principally on fishes, squids, and octopuses near coastlines.

METHODS

The liver and kidneys were selected as the principal tissues for this study because heavy metals tend to accumulate in these organs (DuBois and Geiling, 1959; Curry, 1969). Samples of muscle were collected from fur seals but not from harbor seals.

Collection of Samples

In general, the sampling was conducted as follows: From a seal liver weighing about 1.8 kg, a kidney weighing about 0.5 kg, or muscle from the shoulder area, a sample of about 75 g was placed in a new unwashed glass bottle or polyethylene bag and stored at −23°C. Analyses were made about 5 mo after initial sampling.

Samples included liver and muscle from 3-mo-old pups and 2- and 3-yr-old male fur seals from the Pribilof Islands; liver, muscle, and kidney from fur seals (mostly adult females) from Washington; and liver from harbor seals from California, Oregon, Washington, and the Bering Sea. Tissues from fur seals taken on the Pribilof Islands were kept in polyethylene bags; all other tissues were kept in new glass bottles.

Analyses of Samples

For the analysis of mercury, four replicate 20-mg samples were taken from a piece of tissue in the sample bottle and analyzed. The mean of these four replicates was taken as representative of the particular tissue for that analysis. The analytical procedure for mercury involves introduction of the weighed sample into a tubular furnace from which the products of combustion and vaporized mercury are drawn. After scrubbing and filtering to remove interfering components, the mercury vapor is passed through a cell and read by atomic absorption spectrophotometry.[3]

For lead, cadmium, and arsenic analyses, a separate 2-g sample was taken for each metal. The lead analysis was carried out by digesting the sample in a 5:2 nitric-sulfuric acid mixture followed by dry ashing in a muffle furnace at 550°C until all organic material was removed. Following dissolution in 5 ml of hydrochloric acid, lead content was determined by the double extraction, mixed color dithizone method (Committee on Chemical Procedures of the Occupational Health Section, American Public Health Association, 1955).

For cadmium, the sample was wet ashed in a 2:1 nitric-perchloric acid mixture, and the resultant solution diluted to a known volume with water. The cadmium was extracted into methyl isobutyl ketone (MIBK) by means of chelation with sodium diethyldithiocarbamate (NDDC) and measured by atomic absorption (Berman, 1967).

For arsenic, the sample was wet ashed in an 8:4:1 nitric-perchloric-sulfuric acid mixture to oxidize organic matter and release organically bound arsenic. Following digestion, the sample was diluted to 25 ml volume with water and arsenic determined by the silver diethyldithiocarbamate method (American Public Health Association, 1971).

Detection limits of the analyses were 1 ppb for mercury, 0.1 ppm for lead, 0.01 ppm for cadmium, and 0.2 ppm for arsenic. Recoveries were over 90% for mercury and cadmium where mercury was added as elemental mercury dissolved in nitric acid and cadmium was added as cadmium sulfate. Lead and arsenic recoveries were over 95% with lead added as lead nitrate and arsenic added as arsenic trioxide.

All of the tissue samples were analyzed by Environmental Health Laboratories Inc.,

[3] Hermann, W. J., Jr., J. W. Butler, and R. G. Smith. 1968. A dynamic system for the rapid microdetermination of mercury in undigested biological materials. Presented at Applied Seminar on Laboratory Diagnosis of Diseases Caused by Toxic Agents, Washington, D.C., Nov. 8-9, 1968. Wayne State Univ., Detroit, Mich., Dep. Med., 14 p., 1 fig. (Processed.)

Farmington, Mich.[4] A sample of paper lid liners from the glass bottles was analyzed by the use of neutron activation by Battelle Pacific Northwest Laboratories, Richland, Wash., to determine amounts of mercury, lead, cadmium, and arsenic.

Age Determinations

Ages were assigned to fur seals by counting layers of dentine in sectioned upper canine teeth (Scheffer, 1950; Fiscus, Baines, and Wilke, 1964). Errors in assigning ages to fur seals are small in young seals but increase sharply in animals older than 7 yr (Anas, 1970b). Most errors in older animals, however, are only of a magnitude of ± 2 yr. Although canine teeth of harbor seals have layers of dentine, it is not known if these layers accurately portray age. Ages were not assigned to harbor seals, but body lengths were taken.

RESULTS

Heavy Metals in Fur Seal Tissues

Amounts of total mercury were higher in liver than in muscle or kidney of fur seals (Table 1). Mercury in liver ranged from 0.4 ppm in a fetus taken 3 mo before birth (the liver of the 11-yr-old mother had 86 ppm), to 0.1-0.3 ppm in 10 pups, 3-19 ppm in 30 young males, 7-78 ppm in two young females, and 19-172 ppm in 36 adult females. For muscle, 0.1 ppm was found in five pups, 0.1-0.4 ppm in 29 young males, and 0.2-0.4 ppm in 10 adult females. Mercury in kidney ranged from 0.2 ppm in a fetus (the mother had 1 ppm), to 0.7 ppm in a young male, and 0.6-1.6 ppm in eight females, 1 to 20 yr old.

A wide range of mercury was found only in the liver, so variability due to sampling is more important for liver than for muscle or kidney. The 95% confidence limits of within-sample variability for the 20-mg samples of liver were ± 11% of the mean values. The average variability between seals within ages was 55 times greater than the variability within the 20-mg samples. Thus, to increase accuracy, larger samples of seals are more important than additional 20-mg samples from each piece of liver.

Methylmercury was not determined in this study. However, in samples of liver from California sea lions, about 2% of the total mercury was methylmercury (Buhler, see Footnote 2).

On the average, amounts of lead and cadmium were higher in kidney than in liver (Table 2). Arsenic was not detected in any of the samples. Lead in liver ranged from 0.8 ppm in a fetus (the mother also had 0.8 ppm), to 0.2 ppm in a young male, and 0.4-0.8 ppm in eight females. Lead in kidney ranged from 0.3 ppm in a fetus (0.8 ppm in the mother), to 1.8 ppm in a young male, and 0.8-1.2 ppm in eight females. Cadmium in liver ranged from 0.5 ppm in a fetus (4.6 ppm in the mother), to 0.6 ppm in a young

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1. — Parts per million mercury on a wet weight basis in liver, muscle, and kidney of fur seals taken off Washington and on the Pribilof Islands, 1970-71.

Age (years)	Sex	Area	Year collected	Number of seals	Tissue	Mercury
0.3 (Pups)	Mixed	Pribilof Islands	1970	10	Liver	0.1— 0.3
			1970	5	Muscle	0.1
2-3	Male	Pribilof Islands	1970	29	Liver	3.0— 19.0
			1970	29	Muscle	0.1— 0.4
5-19	Female	Washington Coast	1970	29	Liver	19.0—172.0
			1970	10	Muscle	0.2— 0.4
Fetus	Male	Washington Coast	1971	1	Liver	0.4
			1971	1	Kidney	0.2
1	Male	Washington Coast	1971	1	Liver	3.7
			1971	1	Kidney	0.7
1-20	Female	Washington Coast	1971	8	Liver	7.1—132.0
			1971	8	Kidney	0.6— 1.6

TABLE 2. — Parts per million cadmium and lead on a wet weight basis in kidney and liver of fur seals taken off Washington, 1971.[1]

Age (years) of specimens	Sex of specimens	Kidney		Liver	
		Cadmium	Lead	Cadmium	Lead
Fetus	M	0.1	0.3	0.5	0.8
1	M	1.7	1.8	0.6	0.2
1	F	6.9	0.8	0.9	0.6
3	F	4.3	0.8	2.2	0.6
6	F	15.6	1.2	2.6	0.6
8	F	0.2	0.9	1.2	0.5
11	F	6.2	0.8	4.6	0.8
15	F	9.6	0.9	1.1	0.4
16	F	1.0	1.0	1.7	0.5
20	F	6.8	0.8	1.7	0.7

[1] Arsenic was not found above the limit of detection of 0.2 ppm (mg/kg) in either kidney or liver in any of the samples.

male, and 0.9-4.6 ppm in eight females. Cadmium in kidney ranged from 0.1 ppm in a fetus (6.2 ppm in the mother), to 1.7 ppm in a young male, and 0.2-15.6 ppm in eight females.

Lid liners from new glass bottles had 1.1 ppm mercury and 0.4 ppm arsenic. Lead and cadmium were not detected. The tissues and lid liners were never in direct contact, but some transfer of mercury from the lid liners and glass bottles could have occurred. However, the maximum contribution from the lid liners would have been 0.004 ppm mercury, so the data were not adjusted.

Heavy Metal — Age Comparisons in Fur Seals

Regression equations were computed for samples from fur seals collected in 1970 and 1971 to determine if mercury in liver, muscle, and kidney and if lead and cadmium in liver and kidney were correlated with age. Significant correlations for mercury have been reported for fur seal liver (Anas, 1970a) and whole fishes (Bache, Gutenmann, and Lisk, 1971). Untransformed data were used here because log transformations did not significantly improve the correlations. Fetuses and pups were not included in the calculations. Only liver tissues were collected both in 1970 and 1971. The correlation coefficients in the two years for mercury in liver were common ($P > 0.05$), so the data were pooled. Mercury in liver had a significant positive correlation with age ($P < 0.001$, $r = +0.84$). The data indicate that mercury accumulates in liver. Mercury in muscle and kidney did not correlate with age ($P > 0.05$, $r = +0.05$ and $+0.51$, respectively). Also, lead and cadmium in liver and kidney did not correlate with age ($P > 0.05$, $r = +0.19$ and -0.45 for lead and $r = +0.17$ and $+0.04$ for cadmium in liver and kidney, respectively). Sample sizes were 67 for mercury in liver, 39 for mercury in muscle, and 9 for cadmium and lead in liver and kidney.

Mercury in Harbor Seal Livers

Harbor seals are nonmigratory, so levels of contaminants in this species are useful for locating geographical concentrations of contaminants, provided that the food species do not migrate long distances. Studies suggest that the principal food species of harbor seals do not migrate far (Scheffer and Sperry, 1931; Spalding, 1964; Kenyon, 1965). The highest levels of mercury were found in harbor seals from San Miguel Island (Table 3). One harbor seal from San Miguel Island had 700 ppm mercury in the liver. The amount of mercury in this sample is so much higher than the amounts found in the other seals that the possibility of contamination of the sample should be considered. However, as far as is known, this sample was treated no differently than the other samples. The sample size is small and the ages are not known, but the concentrations of

TABLE 3. — Parts per million mercury on a wet weight basis in liver of harbor seals taken in the eastern Pacific Ocean, 1970-71.

Location	Date collected	Sex	Length (cm)	Mercury
San Miguel Is., Calif.	2 June 1971	F	161	700
	2 June 1971	F	153	81
	4 June 1971	M	176	124
	5 June 1971	F	156	171
Columbia R., Oregon	May 1971	M	—	0.3
	do	M	112	3.2
	do	F	126	68
Washington Coast	2 Sept. 1971	F	84	1.3
Puget Sound, Washington	24 Nov. 1970	M	—	60
	21 June 1971	M	95	12
Pribilof Is., Alaska	17 Aug. 1971	M	135	0.6
	do	F	140	3.2
	do	M	175	8.9

mercury in San Miguel Island seals appear to differ significantly from those from the Pribilof Islands. Except for the one seal with 700 ppm mercury, the amounts of mercury found in harbor seals from all areas studied are within the range of those found in livers of fur seals.

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BIOECONOMIC CONTRIBUTION OF COLUMBIA RIVER HATCHERY COHO SALMON, 1965 AND 1966 BROODS, TO THE PACIFIC SALMON FISHERIES

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ABSTRACT

Marked coho salmon, *Oncorhynchus kisutch*, smolts of the 1965 and 1966 broods were released from 20 hatcheries on four sections of the Columbia River and tributaries. Commercial and sport fisheries in marine waters from Pelican, Alaska, to Avila Beach, Calif., and on the Columbia River were sampled during 1967-69 for marks.

The net value of the estimated total catch of hatchery fish was calculated after adjusting for the effects of marking. Also estimated for each brood were the total costs of rearing including amortized capital outlay. Total benefits of $8.58 million for the 1965 brood and $9.11 million for the 1966 brood were estimated as applicable to normal production years when no marking takes place. Corresponding costs were estimated as $1.29 million for the 1965 brood and $1.23 million for the 1966 brood. Estimated benefit/cost ratios for the 20 Columbia River coho salmon hatcheries, as operated under production regimes prevailing during the study, may prove useful in decisions affecting management policies. The ratios are 6.6/1 for the 1965 brood, 7.4/1 for the 1966 brood, and 7.0/1 for both broods combined.

Use of the Columbia River has expanded tremendously in the past 30 years through Federally financed and/or licensed water use projects. This expansion has depleted valuable stocks of Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, through the loss and deterioration of natural stream habitat. Therefore, mitigative measures—hatcheries, fish ladders, and spawning channels—to supplement the declining natural production of Columbia River salmon and steelhead trout have been Federally funded.

To counteract the severe loss of salmon and steelhead trout environment in the Columbia River basin, the U.S. Government began financing the Columbia River Development Program in 1949. The Program is a cooperative effort of the fish management agencies of the states of Oregon, Washington, and Idaho and the Federal Government. The Columbia Fisheries Program Office, National Marine Fisheries Service, Portland, Oreg., administers the Program, which is designed to increase production of salmon and steelhead in the Columbia River. The Program's major thrust has been to improve the runs of salmon and steelhead by protecting and improving stream environment and by production of fish in hatcheries. The main accomplishment is the construction or modernization of 21 salmon and steelhead hatcheries on the lower Columbia River and tributaries.

There are two major reasons for the concentration of effort on salmon and steelhead trout. First, their life histories allow successful hatchery propagation. Second, these species are historically and economically important to the United States. Annual catches of Pacific salmon have ranked first or second for the past 3 decades in landed value of commercial finfishes to United States fishermen. Chinook salmon, *O. tshawytscha*, and coho salmon, *O. kisutch*, landings have accounted for 35% of the 6-yr average (1966-71) commercial value ($70 million) for salmon—$12.5 million for chinook and $11.9

[1] Columbia River Fisheries Program Office, National Marine Fisheries Service, NOAA, 811 Northeast Oregon St., Portland, OR 97208.
[2] Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98102.

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for coho (Lyles, 1968, 1969; National Marine Fisheries Service, 1971; Riley, 1970, 1971; Wheeland, 1972). In addition, the net economic value of marine and freshwater sport fishing for salmon in the U.S. in 1970 was estimated at $77.7 million. This fishery was made up of 64% coho and 32% chinook.[3]

In 1950 five salmon hatcheries, representing the entire Columbia River production of hatchery coho salmon, released about 1 million juveniles typified by a short rearing period, poor nutrition, and low survival. In contrast, the number of hatcheries rearing coho increased to 20 by 1966-67, and annual releases averaged 20 million smolts. These salmon benefited from advances in fish culture, especially nutrition, applied during the early 1960's and were characteristically large and healthy with a high survival potential (Cleaver, 1969a).

In 1962 the Columbia Fisheries Program Office started a marking study to estimate the contribution of Columbia River hatchery-reared fall chinook salmon to the Pacific coast fisheries. In 1965 this study was expanded to include coho salmon. Accordingly, representative (10%) samples from all Columbia River hatcheries rearing 1965- and 1966-brood coho salmon were marked. Sampling for these marked coho took place from 1967 through 1969 in the sport and commercial fisheries from Alaska to California. A contribution study of this magnitude had never before been undertaken. The information to be gained from this study was critically needed to determine if increased Federal funding for Columbia River hatcheries was economically justified.

The objectives of this report are to (1) describe the design and operations of marking and release procedures, (2) estimate the contribution (catch) to Pacific salmon fisheries during 1967, 1968, and 1969 for the 1965-66 brood coho salmon hatchery releases, and (3) develop benefit/cost ratios for these two broods.

BIOLOGICAL EVALUATION

Experimental Design

Procedures were basically the same as described by Worlund, Wahle, and Zimmer (1969) for the fall chinook salmon study but will be summarized here. The Columbia River was divided into four sections. These sections will be defined later. Releases of marked fish were intended to identify and estimate the catches from each section. Execution of the plan depended, as for the evaluation of fall chinook salmon hatcheries, on the cooperation of many people in the following agencies:

Alaska Department of Fish and Game
Fisheries Research Board of Canada
Washington Department of Fisheries
Fish Commission of Oregon
Oregon State Game Commission
California Department of Fish and Game
National Marine Fisheries Service
Bureau of Sport Fisheries and Wildlife

The basic plan was to mark the same proportion of juvenile coho salmon released at each hatchery and to sample for marks in commercial and sport fisheries. Total catches of fish from all hatcheries then could be estimated from (1) fractions of marked fish in each release, (2) numbers of each type of mark actually recovered, (3) fractions of the total catches sampled for marks by time and area in each fishery, and (4) information on any bias associated with application or detection of marks.

Allocation of Marks

The 20 hatcheries involved in this study are distributed over much of the mainstem Columbia River accessible to anadromous fish (Figure 1). Klaskanine River Salmon Hatchery, the lowermost station, and Leavenworth National Fish Hatchery, the uppermost, are on tributaries about 25 km and 800 km (15 and 500 miles), respectively, above the Columbia River mouth. Some hatcheries (Bonneville, Cascade, OxBow, and Little White Salmon) are adjacent to the main Columbia River and release their fish almost directly into it. In contrast, fish released at the Toutle River station must travel 65 km (40 miles) to reach the Columbia River.

Four different marks were available (from the Pacific Marine Fisheries Commission) for the 1965 brood of coho salmon. The Columbia River was therefore divided into four sections—Lower River, Middle River, Upper River, and Uppermost River—and one mark was assigned to each (Table 1). The adipose-right maxillary

[3] George K. Tanonaka. 1972. A general comparison of the commercial and sport salmon fisheries of the United States, 1940-70. Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash. (Unpubl. manuscr.) 15 p., 7 tables, 4 fig., App. A-B.

FIGURE 1.—Location and grouping by river section of Columbia River hatcheries participating in this study.

mark (Ad-RM) was used for hatcheries in the Lower River section—Columbia River mouth to Cowlitz River. The adipose-only finclip (Ad) was allotted to hatcheries in the Middle River section—the Cowlitz River to Bonneville Dam. Hatcheries in the Upper River section—Bonneville Dam to The Dalles Dam—were issued the adipose-left maxillary mark (Ad-LM). Leavenworth National Fish Hatchery, the only study hatchery in the Uppermost River section—above The Dalles Dam—was assigned the dorsal-adipose finclip (D-Ad).

The same marks were used for the 1966 brood with one exception; at Leavenworth National Fish Hatchery, maxillary marks were added to the D-Ad finclip. Juveniles with D-Ad-RM marks were released at the hatchery and those with D-Ad-LM were trucked downstream and released below Bonneville Dam. The purpose of the two marks and release sites was to examine differential mortality due to passage through dams; results will be treated in a subsequent report.

Sources of Variation and Error

To evaluate variations between broods and river sections, two broods (1965-66) of coho salmon were included in the study, and each river section was allotted a specific mark. Mortality due to marking, the most important source of error, was evaluated by comparing marked/unmarked ratios in hatchery releases and returns. To evaluate the dilution effect of returning wild fish on the marked/unmarked ratio at study hatcheries, oxytetracycline (TM-50) was added to the diet of both broods of coho salmon reared at Big Creek (Ad-RM mark) and Eagle Creek (Ad finclip) hatcheries. Tetracycline deposits a permanent mark on the bone structure of feeding juvenile salmon and, at spawning, this mark is readily detected on coho vertebrae under ultraviolet light (Weber and Ridgway, 1967). Thus, wild coho were identifiable and were subtracted from the total unmarked returns to Big Creek and Eagle Creek hatcheries.

Marked fish were held at Klickitat State Salmon Hatchery to evaluate the degree of mark regeneration. Markers at all participating hatcheries were asked to record naturally missing fins and maxillary bones. Catch samplers were alerted to possible regeneration so they could look for malformed fins.

Rearing techniques at different hatcheries varied within as well as between river sections.

The limited number of marks available precluded individual hatchery comparisons as made from data of the fall chinook salmon study (Cleaver, 1969b; Worlund, Wahle, and Zimmer, 1969; Lander, 1970; Henry, 1971). The size of fish at release reflects partially the differences in rearing techniques. In both wild and hatchery salmon stocks, it is well known that large smolts survive better and contribute more to catches, other factors being reasonably equal, than do small smolts (Ricker, 1962; Fredin, 1964; Johnson, 1970). The average size of fish in releases varied considerably between hatcheries, somewhat between river sections, and slightly between broods. Again, the limited number of marks prevented evaluation of the effect of size at release on contribution, but average weights are included to complete the data record (Appendix Tables 1a and 1b).

Estimating Procedures

Simple numerical examples explain the basic estimating procedures. A more formal account was reported in the chinook salmon study (Worlund, Wahle, and Zimmer, 1969).

The first quantities to be estimated were the numbers of marked and unmarked fish in hatchery releases. This was done with data from a 10-part sampler (see "Marking and Release Procedures"). The device was precalibrated from a number of trials with known numbers of fish to find the average number and percentage retained by a single closed pocket. The following example illustrates the fish enumeration procedure. Suppose a precalibrated pocket is found to remove a 10.1% sample. Also, suppose after passing all the fish in a pond through the sampler, the number of fish retained by the

TABLE 1.—Grouping of Columbia River hatcheries participating in study and type of mark assigned to each group.

River section and hatchery[1]	Hatchery location	Mark[2]
Lower River (Columbia River mouth to Cowlitz River)		
Klaskanine (FCO)	Klaskanine River	Ad-RM
Grays River (WDF)	Grays River	" "
Big Creek (FCO)	Big Creek, Columbia River	" "
Elokomin (WDF)	Elokomin River	" "
Middle River (Cowlitz River to Bonneville Dam)		
Toutle (WDF)	Green River, Toutle River	Ad only
Lower Kalama (WDF)	Hatchery Creek, Kalama River	" "
Kalama Falls (WDF)	Kalama River	" "
Lewis River (WDF)	Lewis River	" "
Speelyai (WDF)	Speelyai Creek, Lewis River	" "
Sandy (FCO)	Cedar Creek, Sandy River	" "
Eagle Creek (FCO)	Eagle Creek, Clackamas River	" "
Washougal (WDF)	Washougal River	" "
Bonneville (FCO)	Tanner Creek, Columbia River	" "
Upper River (Bonneville Dam to The Dalles Dam)		
Cascade (FCO)	Eagle Creek, Columbia River	Ad-LM
OxBow (FCO)	Herman Creek, Columbia River	" "
Carson (BSFW)	Tyee Springs, Wind River	" "
Little White Salmon (BSFW)	Little White Salmon River	" "
Willard (BSFW)	Little White Salmon River	" "
Klickitat (WDF)	Klickitat River	" "
Uppermost River (above The Dalles Dam)		
Leavenworth (BSFW)	Icicle Creek, Wenatchee River	D-Ad D-Ad-LM D-Ad-RM

1/ Acronyms designate the following agencies: FCO = Fish Commission of Oregon, WDF = Washington Department of Fisheries, and BSFW = Bureau of Sport Fisheries and Wildlife.

2/ Ad = adipose finclip, D = dorsal finclip, LM = left maxillary bone clip, and RM = right maxillary clip.

closed pocket is found to be 6,060. The total number of fish in that pond is then estimated as 6,060/0.101 = 60,000. Suppose further that of the 6,060 fish retained by the pocket, 606 fish are found to be marked. Then 606/6,060 = 10% of the estimated 60,000 fish in the pond, or 6,000 fish are estimated to be marked and 54,000 unmarked. The total release, numbers marked and unmarked, and proportion marked were estimated for a hatchery by summing data from all ponds. Finally, estimates of the foregoing quantities for all fish released into a given river section were obtained by summing the estimates for appropriate hatcheries.

To estimate actual recoveries with a certain mark during a specific sampling period in a given fishery, the total catch (of marked and unmarked fish) during that period was multiplied by the fraction of sampled fish observed with that mark during the same period. For example, 16 Ad-RM marks were detected during June 1-30, 1968, from 9,827 coho salmon examined at Crescent City, Calif., in a catch of 31,082 from the commercial troll fishery. Thus, 16/9,827 (approximately 0.2%) of the sample had Ad-RM marks. The total marked catch for that period and landing port was estimated to be about 0.2% of the 31,082 fish caught or 62 Ad-RM marks (actual calculations were carried to eight places to avoid rounding errors). Similar calculations were made for each period. The results then were summed for all periods and appropriate landing locations to estimate the seasonal recovery of a certain mark in the given fishery (e.g., Ad-RM marks in the California troll fishery during 1968).

The catch of unmarked hatchery fish for each ocean sport and commercial fishery, and the Columbia River fisheries, was estimated for each year and brood by dividing the estimated catch of fish having a specific mark by the expected marked/unmarked ratio. The latter was calculated from the ratio at release and the estimated relative survival of marked fish. Suppose an estimated 2,000 1965-brood Ad-RM marks were recovered in 1968 in the California ocean sport fishery, the marked/unmarked ratio was 0.1 for all hatcheries where Ad-RM marks were released, and the survival of marked fish was estimated to be 80% that of unmarked fish; then the estimated catch of unmarked fish would be $(2{,}000)/(0.1 \times 0.80) = 25{,}000$ fish.

The catch of hatchery fish released from a given river section was estimated by summing estimates for marked and unmarked hatchery fish from each type of fishery. Nondetection of certain marks in ocean fisheries complicated the estimation of the hatchery contribution.

The relative survival of marked fish was estimated by comparing marked/unmarked ratios at release and return, as noted earlier for tetracycline (internal) and finclip (external) marking at the Big Creek and Eagle Creek stations. At the Big Creek station for the 1965 brood, for example, the pond sampling procedures just described gave an estimated marked/unmarked ratio at release of 0.12083 (for the Ad-RM finclip). Enumeration at the hatchery of all internally- and externally-marked returns ("jacks" or age 2 males in 1967 plus age 3 males and females in 1968) gave a marked/unmarked ratio of 0.09885. The survival of marked fish between the time of release and at return to the hatchery was therefore estimated to be 0.09885/0.12083 = 0.8181 that of unmarked fish.

With estimates of all these quantities at hand, it remained only to estimate the average weight and unit value of fish caught to calculate their total economic value. Weight data were collected from a predetermined number of fish throughout the season at different landing locations from which a given fishery operated. Resulting means were assumed to be representative.

Assumptions

The foregoing method of estimating catches of hatchery fish requires certain assumptions. These are considered after presentation of the data (see "Bias Associated with Marks" and "SUMMARY"). The main assumptions are:

1. A marked fish is identifiable as a marked fish throughout life.
2. All fish detected and reported with the kind of mark applied are hatchery fish.
3. All coho salmon sampled in ocean fisheries are in their third and final year of life.
4. Marked and unmarked fish have the same maturity schedules.
5. The same proportion of releases is marked at each hatchery in a given river section.
6. Marked and unmarked fish from a given river section are equally vulnerable to capture

(i.e., have the same distribution by time and area).

Field Operations

Marking and Release Procedures

Artificial propagation procedures were similar at all coho salmon hatcheries during the study period. Adults normally returned to the hatcheries during September-November and were spawned during October-November. Fry generally reach the free-swimming stage in March. The fish were released as smolts 13 mo later at an average length of 12-15 cm (4.5-6 inches) and were available during the following year to the fisheries from central British Columbia to central California.

The marking phase of this study began in May 1966 and ended in June 1967. About 10% of the 1965- and 1966-brood coho salmon were marked. A modified sampling tool (Worlund, Wahle, and Zimmer, 1969) was used to obtain a random sample for marking. The "10-part sampler" consisted of a cylindrical liner containing a circular metal frame divided into 10 equal pie-shaped sections with a zipper-bottomed net pocket hung from each section. When a 10% sample was to be taken, the zippers on all but one of the pockets were opened, the frame and liner were placed in a water-filled tub, and about 18 kg (40 pounds) of fish were placed into the liner. The closed net pocket retained the desired sample when the line and frame were lifted. The fish that passed through the open net pockets remained in the tub and were placed into another pond. This procedure was followed until all the coho in each pond were processed.

Fish to be marked were anesthetized with MS-222[4] (tricaine methanesulfonate). The fins and maxillary bones were clipped with bent-nosed scissors. Marked fish were held in hatchery troughs until they recovered from the anesthetic, then returned to the group from which they came. To insure that fins and maxillary bones were actually removed, quality control of marking was maintained by periodic random sampling of the marked fish throughout the marking operation.

[4] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

The entire coho salmon production of each hatchery was sampled to estimate the proportion and numbers of marked fish released. The "10%" samples removed initially by the calibrated pocket were set aside then resampled to obtain a "1%" sample which was sorted into marked and unmarked groups, counted, and weighed. The counts together with an estimate of the proportion removed by the particular pocket of the sampler were used to estimate the numbers of marked and unmarked fish released.

In Table 2, the estimated numbers of marked and unmarked fish released and the percentages marked are summarized for each mark type and brood year. Detailed data for each hatchery are given in Appendix Tables 1a and 1b. Over 40 million coho salmon of both broods were released from the study hatcheries. The number of marked fish released by section for the 1965- and 1966-brood years combined were Lower River, 0.9 million; Middle River, 1.7 million; Upper River, 1.3 million; and Uppermost River, 0.2 million. A total of 39.1 million coho from both broods was released from the study hatcheries in the Lower, Middle, and Upper River sections. Of these, 9.8% were marked. About 0.9 million coho were released from the Uppermost River section, of which 21.1% were marked.

Recovery of Marks in Fisheries

The mark-sampling phase of this study was designed in 1963 for fall chinook salmon and was expanded to include coho in 1967, 1 year before the 1965-brood coho were expected to appear in great numbers in the fishery. This advanced sampling was done for two reasons: (1) to locate the sampling problem areas and correct any deficiencies before the major appearance of the 1965-brood coho in the fisheries and (2) to assist the Washington Department of Fisheries in recovering their marked 1964-brood Puget Sound coho. This phase of the investigation ended in 1969. Catch sampling covered major ocean fisheries from Pelican, Alaska, southward to Avila Beach, Calif., and Columbia River fisheries. Sampling for marks in each area consisted of recording numbers of fish examined for marks and the recoveries of each type of mark detected. Lengths and weights of marked coho salmon from both broods were recorded also. The sampling sea-

TABLE 2.—Estimated numbers, percentage marked, and marked to unmarked ratios of 1965- and 1966-brood coho salmon released from evaluation hatcheries by river sections.

Brood year	River section and (in parentheses) mark	Marked released	Unmarked released	Total released	Proportion marked	Marked/ unmarked
1965	Lower River (Ad-RM)	508,294	4,670,794	5,179,088	0.0981	0.1088
	Middle River (Ad)	845,674	7,895,360	8,741,034	0.0967	0.1071
	Upper River (Ad-LM)	837,829	7,670,539	8,508,368	0.0985	0.1092
	Uppermost River (D-Ad)	101,734	402,272	504,006	0.2018	0.2529
	Subtotal 1965 brood	2,293,531	20,638,965	22,932,496	0.1000	0.1111
1966	Lower River (Ad-RM)	385,630	3,569,807	3,955,437	0.0975	0.1080
	Middle River (Ad)	764,262	6,965,703	7,729,965	0.0989	0.1097
	Upper River (Ad-LM)	493,110	4,544,676	5,037,786	0.0979	0.1085
	Uppermost River (D-Ad-LM)[1/]	96,643	466	97,109	0.9952	207.3884
	Uppermost River (D-Ad-RM)	78,092	269,355	347,447	0.2248	0.2899
	Subtotal 1966 brood	1,817,737	15,350,007	17,167,744	0.1059	0.1184
	TOTAL BOTH BROODS	4,111,268	35,988,972	40,100,240	0.1025	0.1142

1/ Released below Bonneville Dam.

sons were stratified into relatively small time units (usually 2-wk periods).

The main fisheries sampled were ocean sport and commercial, Columbia River sport and commercial, and Puget Sound fisheries. The ocean fisheries were stratified further by port of landing. The Alaska and British Columbia troll, purse seine, and gillnet fisheries; Columbia River commercial and sport fisheries; and Puget Sound sport and commercial fisheries were stratified by area of catch. The specific fisheries sampled are listed in Table 3 and shown in Figure 2.

Catch data for each time-location stratum were provided by management agencies. The catch of coho salmon in numbers of fish was an estimate for most fisheries. Commercial catches were estimated either from (1) the total weight of landings and an estimate of average fish size or (2) total salmon landings (numbers) and an estimate of species composition. Estimates of sport catches were from measures of total effort and catch per unit of effort or from salmon punch cards together with independent sampling by the management agency.

About 20% of each time-location stratum was sampled for marks. Table 4 gives the annual total catch of both broods of coho salmon by year and number sampled for marks each year. During the 3 years of sampling, 15.4% of the total catch of 21.1 million coho were examined for marks. The actual mark sampling percentages were 18.3, 13.5, and 14.3% for 1967, 1968, and 1969, respectively.

Enumeration of Returns to Hatcheries

An estimate of the numbers returning to hatcheries was required to measure the total hatchery output and marking mortality. All returns to most hatcheries were examined for marks; at some hatcheries, the numbers marked and unmarked were calculated after a known percentage of the total return was sampled for marks. A breakdown of the returns to each of the study hatcheries is in Appendix Tables 2a and 2b.

Estimation of Total Catch from Hatcheries

Actual Recoveries

Tables 5a and 5b summarize marked recoveries by brood year, mark, year of recovery,

TABLE 3.—Areas where catches were examined for marked coho salmon of Columbia River origin by port or zone of landing and type of fishery.

Area sampled	Type of fishery				
	Sport	Commercial			
	Rod and reel	Troll	Gill net	Dip net	Purse seine
British Columbia		Alaska area, Zones 29, 40-43, and Area C.[1]	Zones 29, 40-43		Zones 40-43.
Washington ocean	Sekiu	Seattle	Grays Harbor.		
	Neah Bay	Neah Bay	Willapa Bay.		
	LaPush	LaPush.			
	Westport	Westport.			
	Ilwaco	Ilwaco.			
Puget Sound and Juan de Fuca Strait	Zones 6-12		Zones 1-15		Zones 1-12.
Oregon ocean	Warrenton	Astoria.			
	Tillamook	Tillamook.			
	Pacific City	Pacific City.			
	Depoe Bay	Depoe Bay.			
	Newport	Newport.			
	Florence	Florence.			
	Winchester Bay	Winchester Bay.			
	Coos Bay	Coos Bay.			
	Gold Beach	Bandon.			
	Brookings	Port Orford.			
		Gold Beach.			
		Brookings.			
California ocean	Crescent City	Crescent City.			
	Trinidad	Trinidad.			
	Eureka	Eureka.			
	Shelter Cove	Fort Bragg.			
	Fort Bragg	Albion.			
	Albion	Point Arena.			
	Bodega Bay	Bodega Bay.			
	San Francisco	Point Reyes.			
	Half Moon Bay	San Francisco.			
	Santa Cruz	Half Moon Bay.			
	Monterey	Moss Landing.			
	Morro Bay	Monterey.			
	Avila	Morro Bay.			
		Avila.			
Columbia River and tributaries	Zones 1-6		Zones 1-7	Klickitat River.	
	Cowlitz River.				
	Kalama River.				
	Lewis River.				
	Toutle River.				
	Washougal River.				

1/ Canadian catch 3-12 miles off Washington, Oregon, and California.

river section of origin, and fishery. All marks from the Uppermost River section (Leavenworth Hatchery in Appendix Table 4) are combined as D-Ad marks in Table 5b. During the 3 years of sampling, 37,632 marked coho salmon were recovered. More marked 1965- than 1966-brood coho were caught, but more were released from the 1965 brood. Carson National Fish Hatchery and OxBow Salmon Hatchery, while participating in the study for the 1965 brood, did not do so for the 1966 brood (Table 2). The fraction of marked releases actually recovered for the 1965 brood, 0.0089, was slightly less than for the 1966 brood, 0.0093 (Tables 2, 5a, and 5b).

Estimated Recoveries

As explained under "Estimating Procedures," the total catch of fish with a particular mark was estimated for each stratum (fishery, port of landing or area of capture, and time period) from actual mark recoveries and the sampling fraction. It was assumed that a random sample of coho salmon was examined in each stratum and that in each sample all the marked fish were inspected. The total catch for each mark in each fishery was estimated by summing over the time periods and appropriate ports of landing or areas of capture.

The estimated catches and hatchery returns

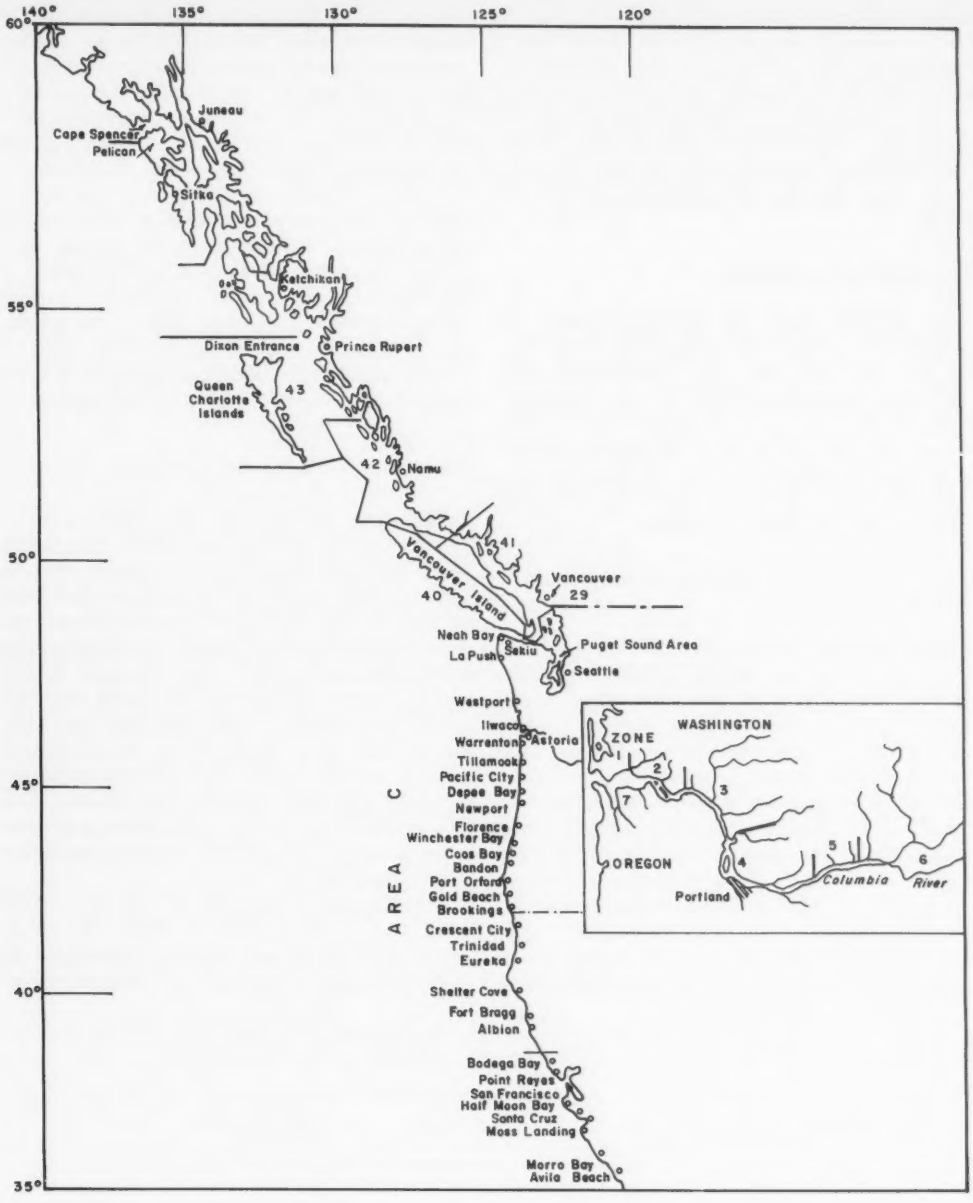

FIGURE 2.—Ports and zones sampled for marked coho salmon of Columbia River origin.

of marked fish are summarized in Tables 6a and 6b by region of recovery, fishery, brood year, and mark. The marks from the Uppermost River section (Appendix Table 5a) are combined in Table 6b. The total estimated catch of marked fish from both broods was 179,096. A total of 33,910 marked coho salmon returned to the study hatcheries during the 3 yr of sampling.

Bias Associated with Marks

To proceed from the estimated catch of marked fish to the total catch of hatchery fish, we must be sure that our assumptions (see "EXPERIMENTAL DESIGN") are satisfied. Some elements (e.g., loss of maxillary bones due to hooking, loss of fins due to injury) cannot be evaluated; others (e.g., mark regeneration, natural marks, relative survival of marked fish) can be appraised more adequately.

Mark Regeneration (Assumption 1) and Quality of Marking

We have three indications of the permanence of fin and maxillary marks. First, about 550 marked coho salmon of the 1966 brood were held for 2 yr at the Klickitat station for fin regeneration studies. We examined these fish periodically throughout the retention period and observed no adipose regeneration. However, we noted a 4.5% complete maxillary regeneration. Second, the appearance of D-Ad marks in the releases of the 1966-brood coho from Leavenworth National Fish Hatchery indicated maxillary regeneration; the maxillary bone was clipped from all 1966-brood Leavenworth coho marked, yet 5% of the marked coho released had only a D-Ad finclip. During marking of the Leavenworth coho, 100 marked fish per marker were examined at irregular periods each day to check mark quality. No unclipped maxillaries were observed. This caused us to disregard failure to clip maxillaries as a reason for the appearance of the D-Ad marks. Therefore, we believe the D-Ad marks occurred mainly because of maxillary regeneration. Finally, the percentage of D-Ad-only marks in the 1969 lower Columbia River commercial catch of 1966-brood Leavenworth Hatchery marked fish was 6.5%. This is very close to the percentage of D-Ad-only marks in the release. Because of these indications, we are assuming that mark regeneration caused little bias in this study.

Natural Marks (Assumption 2)

The catch of hatchery fish would be overestimated if marks identical to those used in this study occurred naturally. To ensure that no natural marks existed in hatchery stocks, coho salmon returns at most Columbia River and some Puget Sound hatcheries were examined for 2 yr before the study. Approximately 35,000 returns were examined and no marks identical to those we planned to use were observed. Also, fish markers at all participating hatcheries examined approximately 3.5 million coho for naturally missing fins and maxillary bones. Only 26 were found to have naturally missing adipose fins and none had naturally missing dorsal fins or maxillary bones.

The possible occurrence of natural marks from other river systems is more difficult to evaluate. Comparisons of the percentage of each mark caught in the lower Columbia River

TABLE 4.—Estimated catches of coho salmon and number of fish examined for marks, 1967-69.[1]

Year	Catch of coho salmon			Sampled for marks
	1965 brood	1966 brood	All ages	
1967	22,946	0	7,539,255	1,381,255
1968	8,587,969	20,457	8,608,426	1,158,932
1969	0	4,933,706	4,966,589	710,753
Total	8,610,915	4,954,163	21,114,270	3,250,940

1/ From all areas sampled (Table 3).

TABLE 5a.—Number of marked 1965-brood Columbia River coho salmon by release section recovered in the fisheries by year, region of capture, and type of fishery, 1967-68.

River section and (in parentheses) mark	Year	California		Oregon		Washington (without Puget Sound)		Puget Sound		British Columbia	S. E. Alaska	Columbia River				TOTALS
		Sport	Commercial	Sport	Commercial	Sport	Commercial	Sport	Commercial	Commercial	Commercial	Sport		Commercial		
												Main	Trib.	Gill net	Dip net	
Lower River (Ad-RM)	1967	0	0	0	0	0	0	0	0	0	0	1	0	15	0	16
	1968	101	491	135	1,049	212	401	0	5	72	*	0	3	107	5	2,581
Middle River (Ad)	1967	0	0	0	0	0	0	0	0	0	0	4	20	1	0	25
	1968	156	968	1,822	5,106	2,187	3,339	0	67	790	*	2	41	778	1	15,257
Upper River (Ad-LM)	1967	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1968	16	131	77	697	324	489	0	1	65	*	0	0	180	65	2,045
Uppermost River (D-Ad)	1967	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
	1968	6	23	52	194	119	144	0	0	9	*	0	0	67	0	614
TOTALS	1967	0	0	0	0	0	0	0	0	0	0	5	20	18	0	43
	1968	279	1,613	2,086	7,046	2,842	4,373	0	73	936	*	2	44	1,132	71	20,497

*No sampling.

TABLE 5b.—Number of marked 1966-brood Columbia River coho salmon by release section recovered in the fisheries by year, region of capture, and type of fishery, 1968-69.

River section and (in parentheses) mark	Year	California		Oregon		Washington (without Puget Sound)		Puget Sound		British Columbia	S. E. Alaska	Columbia River				TOTALS
		Sport	Commercial	Sport	Commercial	Sport	Commercial	Sport	Commercial	Commercial	Commercial	Sport		Commercial		
												Main	Trib.	Gill net	Dip net	
Lower River (Ad-RM)	1968	0	0	0	0	0	0	0	0	0	*	1	2	6	0	9
	1969	22	158	107	911	482	432	0	1	32	*	0	1	158	3	2,307
Middle River (Ad)	1968	0	0	0	0	0	0	0	0	0	*	17	34	12	0	63
	1969	191	905	1,578	4,479	2,120	1,865	2	15	312	*	1	33	759	18	12,278
Upper River (Ad-LM)	1968	0	0	0	0	0	0	0	0	0	*	2	1	6	16	25
	1969	14	102	86	662	525	356	0	1	9	*	0	1	233	53	2,042
Uppermost River (D-Ad)	1968	0	0	0	0	0	0	0	0	0	*	0	0	3	0	3
	1969	6	40	31	118	52	67	0	0	1	*	0	0	50	0	365
TOTALS	1968	0	0	0	0	0	0	0	0	0	*	20	37	27	16	100
	1969	233	1,205	1,802	6,170	3,179	2,720	2	17	354	*	1	35	1,200	74	16,992

*No sampling.

commercial fishery with the percentage of each mark caught in each ocean fishery give an indication of the occurrence of natural marks. After making these comparisons, we noted a preponderance of Ad-only marks especially in the Oregon sport fishery for the 1965 brood and the California sport and commercial fisheries for the 1966 brood. In these fisheries, we observed

TABLE 6a.—Estimated number of marked 1965-brood coho salmon in catches and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1967-68.

Region	Fishery type	D-Ad		Ad-LM		Ad		Ad-RM		Total	
		1967	1968	1967	1968	1967	1968	1967	1968	1967	1968
Ocean fisheries:											
British Columbia.....	Commercial...	0	46	0	459	0	6,339	0	581	0	7,425
Washington.....	Sport.....	0	677	0	1,809	0	11,490	0	1,206	0	15,182
	Commercial...	0	636	0	2,051	0	14,382	0	1,716	0	18,785
Oregon.....	Sport.....	0	226	0	265	0	7,944	0	420	0	8,855
	Commercial...	0	736	0	2,530	0	17,821	0	3,564	0	24,651
California.....	Sport.....	0	18	0	30	0	299	0	331	0	678
	Commercial...	0	109	0	789	0	5,554	0	2,617	0	9,069
Subtotal.....	Sport.....	0	921	0	2,104	0	19,733	0	1,957	0	24,715
	Commercial...	0	1,527	0	5,829	0	44,096	0	8,478	0	59,930
Freshwater fisheries:											
Columbia River.....	Sport.....	0	0	0	0	344	290	25	16	369	306
	Commercial...	7	238	0	846	2	4,907	130	825	139	6,816
Total.....	All fisheries	7	2,686	0	8,779	346	69,026	155	11,276	508	91,767
Columbia River escapement:											
Study hatcheries.....		38	138	1,125	1,882	4,391	9,399	1,568	1,864	7,122	13,283

TABLE 6b.—Estimated number of marked 1966-brood coho salmon in catches and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1968-69.

Region	Fishery type	D-Ad		Ad-LM		Ad		Ad-RM		Total	
		1968	1969	1968	1969	1968	1969	1968	1969	1968	1969
Ocean fisheries:											
British Columbia.....	Commercial...	0	7	0	77	0	2,970	0	278	0	3,332
Washington.....	Sport.....	0	242	0	2,333	0	9,324	0	2,178	0	14,077
	Commercial...	0	281	0	1,456	0	7,782	0	1,807	0	11,326
Oregon.....	Sport.....	0	148	0	392	0	7,304	0	492	0	8,336
	Commercial...	0	645	0	2,930	0	19,952	0	4,261	0	27,788
California.....	Sport.....	0	23	0	38	0	611	0	58	0	730
	Commercial...	0	224	0	465	0	6,024	0	728	0	7,441
Subtotal.....	Sport.....	0	413	0	2,763	0	17,239	0	2,728	0	23,143
	Commercial...	0	1,157	0	4,928	0	36,728	0	7,074	0	49,887
Freshwater fisheries:											
Columbia River.....	Sport.....	0	0	45	35	541	397	31	20	617	452
	Commercial...	6	283	58	2,470	125	8,104	57	1,619	246	12,476
Total.....	All fisheries	6	1,853	103	10,196	666	62,468	88	11,441	863	85,958
Columbia River escapement:											
Study hatcheries.....		8	0	624	1,075	2,191	5,769	2,067	1,771	4,890	8,615

samplers recording partially regenerated Ad-LM and Ad-RM as Ad-only marks. We attribute the preponderance of Ad-only marks in the above mentioned fisheries to the reluctance of samplers to distinguish between partially regenerated maxillaries and maxillaries lost through injury.

Age and Maturity Schedules (Assumptions 3 and 4)

Godfrey (1965) noted that ocean catches of coho salmon in the regions sampled in this study are all, or nearly all, age 3 adults. Johnson (1970) estimated that the ocean catch of

marked 1964-brood coho from Big Creek Hatchery (Figure 1) contained only 3% age 2 coho. This available evidence indicates that Assumption 3 (all coho in ocean fisheries are in their third and final year of life) is reasonably satisfied.

A comparison was made of marked and unmarked returns (Appendix Tables 2a and 2b) to hatcheries in the same river section where released to test Assumption 4 (marked and unmarked fish have the same maturity schedules). Appendix Table 3 shows the percent of 2-yr-old coho salmon in the marked and unmarked returns by river section and brood year. Unmarked strays to other river sections could not be identified by origin, so it was necessary to assume that straying was the same for marked and unmarked returns. The D-Ad comparison (Leavenworth Hatchery) was not made because passage difficulties at John Day Dam in 1969 led to no returns of adults to Leavenworth Hatchery. The nearly equal percentages of 2-yr-olds in the marked and unmarked returns by river section and brood year indicate that Assumption 4 is satisfied.

Marked Proportions at Release and Capture (Assumptions 5 and 6)

Inspection of mark proportion data in Appendix Tables 1a and 1b shows the variability between hatcheries to be small enough to consider Assumption 5 (same proportion of releases marked at each hatchery in a given river section) reasonably well satisfied. At present, no data exist to support Assumption 6 (equal vulnerability to capture for marked and unmarked fish from a given river section), but it is intuitively satisfied. Fish marked by clipping maxillary bones and/or the adipose fin would not seem to be more vulnerable to capture by fishing gear than unmarked fish.

Relative Survival of Marked Fish

Worlund, Wahle, and Zimmer (1969) found that marked fall chinook salmon did not survive as well as unmarked chinook. We also found this for coho salmon. To determine the unmarked catch of hatchery fish, we must account for the lower survival of marked fish. The relative survival values for both broods and each mark type of coho were calculated as explained under "Estimating Procedures." Oxytetracycline (TM-50) was used to mark both broods of coho at Eagle Creek and Big Creek hatcheries to obtain survival values for Ad and Ad-RM marked coho, respectively. Returns to three hatcheries, Little White Salmon, Cascade, and Klaskanine, on streams having no wild spawning populations were used to obtain relative survival values for both broods of Ad-LM and Ad-RM marked coho. Finally, the marked to unmarked ratios at release and return for each river section were combined to obtain survival values for each mark type in both brood years.

The relative survival estimates are in Appendix Table 6. Marked coho salmon that strayed to sections other than where they were released (Appendix Tables 2a and 2b) were excluded from the marked returns in computing relative survival (see "Bias Associated with Marks"). Therefore, the median value for each of the mark types for both brood years combined was arbitrarily used to obtain reasonable approximations for relative survival. The same value was used for Ad-LM and Ad-RM marked coho. The median values for the Ad-only and Ad-maxillary marked coho were 89 and 72%, respectively.

The relative survival of D-Ad marked 1965-brood coho salmon from Leavenworth National Fish Hatchery (Uppermost section) was obtained from TM-50 marking data. In 1967 and 1968, a total of 174 D-Ad-TM-50 marked and 1,305 TM-50-only marked 1965-brood coho returned to Leavenworth. From these values, the marked to unmarked relative survival of 1965-brood D-Ad marked coho was calculated to be 53%. Few hatchery returns of 1966-brood Leavenworth coho were obtained because of passage difficulties at John Day Dam due to construction of fish ladders and mortalities caused by trapping at Priest Rapids Dam. Hence, a relative survival estimate for the D-Ad-RM and D-Ad-LM marks could not be calculated. The value for the D-Ad marked 1965-brood coho (53%) was therefore used to estimate the 1966-brood Leavenworth catch of unmarked fish.

Final Estimates Corrected for Marking

One marked fish represented about 9 unmarked ones at release but about 11-20 (depending on the mark) at return (Tables 2, 6a, and 6b). The foregoing estimates of relative survival for unmarked fish were applied (see "Estimating

Procedures") to estimate the catch of unmarked hatchery fish, then marked fish were added to estimate the total catch.

An additional calculation was required before estimating the unmarked catch associated with the marked 1966-brood Leavenworth Hatchery fish because of the recovery of 1966 brood D-Ad-only marks. The recovery was due to either regeneration or nondetection of D-Ad-maxillary marks (see "Bias Associated with Marks"). Therefore the estimated catch of 1966 brood D-Ad marks had to be apportioned between the estimated catches of D-Ad-RM and D-Ad-LM marks before calculating the catch of unmarked 1966-brood fish. The D-Ad marks were apportioned by the ratio of their occurrence at the time of release. At Leavenworth Hatchery, 5,081 D-Ad marks were estimated to have been released with the D-Ad-RM marks. Below Bonneville Dam, 4,393 D-Ad marks were estimated to have been released with the D-Ad-LM marks. This is a total release of 9,474 D-Ad marks of which 54% (5,081/9,474) came from D-Ad-RM marks and 46% (4,393/9,474) came from D-Ad-LM marks. These ratios were used to apportion the estimated catch of 666 D-Ad marks (Appendix Table 5a) between the D-Ad-RM and D-Ad-LM marked fish in each of the fisheries. For example, 88 D-Ad marked coho (Appendix Table 5a) were estimated to have been caught in the Washington sport fisheries in 1969. Using the occurrence percentages of the D-Ad marks at release, $88 \times 0.54 = 48$ were calculated to be from D-Ad-RM marks and $88 \times 0.46 = 40$ were calculated to be from D-Ad-LM marks. This apportioning was done for each fishery and results are in Appendix Table 4b.

The estimated catches of marked fish used to calculate the catches of unmarked hatchery fish are in (1) Table 6a for the estimated 1965 brood D-Ad, Ad-LM, Ad, and Ad-RM marks captured in the ocean and Columbia River fisheries; (2) Table 6b for the estimated ocean and Columbia River catches of 1966 brood Ad-LM, Ad, and Ad-RM marked fish; and (3) Appendix Table 5b for the catches of marked 1966-brood Leavenworth coho salmon. Appendix Table 7 presents the resulting estimated catches of unmarked hatchery fish.

The estimated total catch of Columbia River hatchery fish (Appendix Table 8) was obtained by adding the estimated catch of marked fish (Tables 6a and 6b) to the estimated unmarked catches (Appendix Table 7). The resulting catch estimates may affect management decisions in years when no marking studies take place. Therefore, as a final step, we divided the estimated catch of each mark in each fishery (Tables 6a and 6b) by the estimated relative survival for that mark (see "Relative Survival of Marked Fish") to obtain a theoretical catch of marked fish assuming no marking mortality. The results were then added to the estimated unmarked catch (Appendix Table 7) to obtain a theoretical total catch of Columbia River hatchery coho salmon. The results are in Table 7 by region of recovery, type of fishery, and year of capture. The table includes the estimated sport catches of hatchery fish in Columbia River tributaries where no creel census took place. This is broken down in detail by year of capture, brood, and stream in Appendix Table 9.

An estimated total of 2,188,172 Columbia River hatchery coho would have been caught during the 3 years of sampling had no marking taken place. This is about 16% of the total catch in areas sampled (Table 3) of 1965- and 1966-brood coho caught during 1967-69 (Table 4)—13% for the 1965 brood and 21% for the 1966 brood. Another useful statistic is the catch/1,000 fish released. For the combined 1965 and 1966 broods, this was 55/1,000—50/1,000 for the 1965 brood and 61/1,000 for the 1966 brood (Tables 2 and 7).

ECONOMIC EVALUATION

A main purpose of this paper is to develop benefit/cost ratios for the 1965 and 1966 broods of coho salmon from Columbia River hatcheries. To develop these ratios, estimates must be made of (1) the costs of rearing the 40.1 million smolts released (Table 2) and (2) the value of the theoretical catch of 2,188,172 coho (Table 7). The rearing costs will be presented first.

Cost Accounting

Production costs are broken down into two categories: (1) amortized construction costs or capital costs and (2) operational costs.

Capital

The "annual imputed capital charge" for each hatchery was computed by amortizing the capital expenditures at each hatchery into 30 equal

TABLE 7.—Theoretical catch of 1965- and 1966-brood hatchery coho salmon by region of recovery, type of fishery, and year of capture, 1967-1969.[1]

Region	Fishery type	1965 brood			1966 brood		
		1967	1968	Total	1968	1969	Total
Ocean fisheries:							
British Columbia.....	Commercial...	0	88,755	88,755	0	38,824	38,824
Washington.....	Sport.....	0	182,372	182,372	0	171,035	171,035
	Commercial...	0	226,212	226,212	0	136,016	136,016
Oregon.....	Sport.....	0	104,063	104,063	0	96,371	96,371
	Commercial...	0	300,004	300,004	0	332,075	332,075
California.....	Sport.....	0	8,750	8,750	0	8,393	8,393
	Commercial...	0	113,700	113,700	0	86,573	86,573
Subtotal.....	Sport.....	0	295,185	295,185	0	275,799	275,799
	Commercial...	0	728,671	728,671	0	593,488	593,488
Freshwater fisheries:							
Columbia River.....	Sport.....	18,739	10,627	29,366	15,584	10,855	26,439
	Commercial...	1,929	82,831	84,760	3,087	151,377	154,464
Total.....	All fisheries	20,668	1,117,314	1,137,982	18,671	1,031,519	1,050,190

1/ Corrected for differential finclip mortality and assuming no marking had taken place.

annual payments using an interest rate of 3.5% .[5] This rate was the average 3- to 5-yr government bond interest rate weighted by the total annual capital outlay at all hatcheries from 1949 (inception of Columbia River Development Program) through 1970. All outlays prior to this period are assumed to be depreciated out completely. The imputed capital charge for each study hatchery was apportioned among the broods and species present by using the percentage of time spent caring for each group of fish. The total annual imputed capital charges for the 1965- and 1966-brood coho salmon are $271,600 and $235,600, respectively.

Operation

The operation and maintenance costs at each hatchery are divided into two categories. They are fish food and drugs and other operational costs. The cost of fish food and drugs is apportioned between each brood and species according to the pounds of each brood and species produced. The operational costs other than food and drugs include costs for labor, personal services, travel, transportation of items, communication services, equipment, supplies and materials, and administration. These costs are allocated to each brood and species in the same manner as the capital costs. The operational costs apportioned to the 1965- and 1966-brood coho are $1,020,700 and $991,000, respectively. The total costs applicable to rearing the 1965- and 1966-brood coho are then $1,292,300 and $1,226,600, respectively.

Benefits

To determine the benefit provided by hatchery releases of 1965- and 1966-brood coho salmon to the commercial and sport fisheries, an estimate of the net economic value to these fisheries must be made. Additional information is critically needed to improve the basis for estimating values for fishery resources; however, the values used in this report are based on the best information now available and the limitations of these values are discussed.

Commercial

Ex-vessel market prices have been used to represent estimated net values for commercially caught fish. There are two quite different reasons why this method can provide satisfactory estimates.

The Columbia River salmon production from hatcheries included in this study provide only a portion of the total salmon production. Use of the ex-vessel price in the standard benefit-cost technique would require the deduction of all associated costs. However, excess capacity typically exists in the fishing sector, so little or

[5] The "annual imputed capital charge" is the estimated cost of government funds over the life of the project.

no additional fishing effort would be needed to land the production from these hatcheries. While this provides an adequate reason to omit fishing costs for hatchery fish, this would not be true for total salmon production.

A stronger basis for omitting costs necessary to land fish and using the ex-vessel price, results from current fishery management policies. Regulated inefficiency has been used in salmon fisheries to prevent overharvest thus excluding efficient fishing methods. This process probably results in dissipation of at least 75% of potential net benefits and may be as high as 95% (Richards, 1969).[6] Since the market prices used result from normal market activities and thus represent the market value of the fish resource to users, this potential benefit could be realized if society elects to change management methods and reduce fishing costs.

Several inadequacies exist in the use of the ex-vessel price as a representation of the net value for commercially caught fish. The first inadequacy is that the ex-vessel market price fails to completely measure market value. Gear or supplies furnished by processors and bonuses paid are examples of values that are not included in estimated market values. A second inadequacy exists since ex-vessel values fail to completely measure potential production. For example, a large share of the catch is now taken on troll gear and many sublegal size fish are caught. In the removal from the gear and release of these sublegal fish, many sustain injuries that result in death or reduced growth. This wastage significantly reduces the total production from the resource to society. Also, estimated market values do not include other types of benefits. For example, ex-vessel prices may not always be determined in markets with adequate competition to indicate total benefits, resulting in a producer surplus (i.e., additional profits to fish buyers). Benefits due to employment and income generated for coastal communities and the regional and national economy are not included. Consumer surplus or benefits to consumers that are not included in market prices are also omitted.

These factors indicate that using the ex-vessel price for commercially caught fish is a reasonable estimate of benefits that could be realized. If all factors were included, this could prove to be a quite conservative estimate of total benefits.

Tables 8a and 8b present the net value of commercially caught 1965- and 1966-brood coho salmon by ocean regions and Columbia River commercial fisheries. Two calculations were required to obtain the net value. The theoretical commercial catch was multiplied by the average Ad marked coho weight to obtain the total pounds of Columbia River coho caught by region. The total pounds were then multiplied by the average ex-vessel price paid in each region to obtain the net value of the coho catch to that region.

Sport

The net value for salmon and steelhead sport fishing is estimated to be $20 per day of fishing. This value results from reconciling the existing research that is closely related to estimated net economic values of Columbia River sport caught salmon. The maximum potential benefits from sport fishing at a single market price is predicted at $20 per fishing day by Brown, Singh, and Richards (1972).[7] A single market price is intended to be comparable with typical conditions that underlie normal market price determination. The original data for this report were from a 1962 survey in Oregon with results published in 1964. The net value that resulted in maximum benefits was estimated at $8 per day of fishing in the original analysis (Brown, Singh, and Castle, 1964). However, Brown and Nawas (in press) developed research techniques that more efficiently utilize available information. When these techniques were used in an analysis of the 1962 survey data, an estimated value of $20 per day was derived. This is the estimated value used in this report.

Two other reports support the revised Oregon results. The estimated net economic value for the 1967 sport salmon fisheries of Washington resulted in a recommended value of $28 per day of fishing (Mathews and Brown, 1970). An evaluation of the net economic values for the Idaho sport fisheries, based on a 1968 survey, resulted

[6] Jack A. Richards. 1969. An economic evaluation of Columbia River anadromous fish programs. U.S. Dep. Int., Fish Wildl. Serv., Bur. Commer. Fish., Working paper 17, 274 p. (Processed.)

[7] William G. Brown, Ashok K. Singh, and Jack A. Richards. 1972. Influence of improved estimating techniques on predicted net economic values for salmon and steelhead. (Oreg. State Univ., Corvallis), Agric. Exp. Stn. unpubl. manuscr., 26 p. (Typescript.)

TABLE 8a.—Estimated value of the theoretical catch of 1965-brood coho salmon from Columbia River hatcheries.

Region	Fishery type	Age	Fish	Sample size	Average weight[1]		Total weight		Value per unit catch[2] [3]	Total value
			Number	Number of fish	Lbs.	Kg.	Lbs.	Kg.	Dollars	Dollars
Ocean fisheries:										
British Columbia.....	Commercial...	3	88,755	143	5.5	2.5	488,152	221,888	0.45	$ 219,668
Washington.....	Sport.....	3	182,372						15.82	2,885,125
	Commercial...	3	226,212	--[5]	5.5	2.5	1,244,166	565,530	0.45	559,875
Oregon.....	Sport.....	3	104,063						20.53	2,136,413
	Commercial...	3	300,004	386	5.6	2.5	1,680,022	750,010	0.45	756,010
California.....	Sport.....	3	8,750						19.01	166,338
	Commercial...	3	113,700	272	6.3	2.9	716,310	329,730	0.45	322,340
Subtotal.....	Sport.....	3	295,185							5,187,876
	Commercial...	3	728,671				4,128,650	1,867,158		1,857,893
Freshwater fisheries:										
Columbia River.....	Sport.....	2	18,739						42.02	787,412
		3	10,627						46.51	494,262
Zones 1-5 & 7.....	Commercial...	2	1,883	--[6]	3.0	1.4	5,649	2,636	0.26	1,469
		3	78,825	385	7.8	3.5	614,835	275,888	0.28	172,154
Indian fisheries[4].....	Commercial...	2	46	--[6]	3.0	1.4	138	64	0.18	25
		3	4,006	--[7]	7.8	3.5	31,247	14,021	0.24	7,499
Subtotal.....	Sport.....	2&3	29,366							1,281,674
	Commercial...	2&3	84,760				651,869	292,609		181,147
Total.....	All fisheries		1,137,982							8,508,590

1/ Weights for ocean commercial fisheries are dressed weights and those for Columbia River fisheries are round weights. Original weights are in pounds for Ad marked fish.

2/ Entries for Washington and Columbia River fisheries (dollars per pound) were obtained from Dale Ward, Washington State Department of Fisheries (personal communication). Washington price was used for British Columbia and Oregon commercial fisheries. Entry for California was obtained from Pat O'Brien, California Department of Fish and Game (personal communication).

3/ The value of a sport caught coho is based on a value of $20.00 per angler day divided by the catch per angler.

4/ Columbia River set net and dip net fisheries and Klickitat River dip net fishery.

5/ No sampling for weight was done in the Washington commercial fisheries. Average weight obtained from Sam Wright, Washington Department of Fisheries (personal communication).

6/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight obtained from Paul Hirose, Fish Commission of Oregon (personal communication).

7/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight from zones 1-5 used.

TABLE 8b.—Estimated value of the theoretical catch of 1966-brood coho salmon from Columbia River hatcheries.

Region	Fishery type	Age	Fish	Sample size	Average weight[1]		Total weight		Value per unit catch[2][3]	Total value
			Number	Number of fish	Lbs.	Kg.	Lbs.	Kg.	Dollars	Dollars
Ocean fisheries:										
British Columbia.....	Commercial...	3	38,824	100	5.8	2.6	225,179	100,942	0.48	$ 108,086
Washington.....	Sport.....	3	171,035	----------					18.05	3,087,182
	Commercial...	3	136,016	--[5]	6.2	2.8	843,299	380,845	0.48	404,784
Oregon.....	Sport.....	3	96,371	----------					24.94	2,403,493
	Commercial...	3	332,075	331	5.7	2.6	1,892,828	863,395	0.48	908,557
California.....	Sport.....	3	8,393	----------					19.92	167,189
	Commercial...	3	86,573	92	6.3	2.9	545,410	251,062	0.48	261,797
Subtotal.....	Sport.....	3	275,799	----------					-----	5,657,864
	Commercial...	3	593,488	----------			3,506,716	1,596,244	-----	1,683,224
Freshwater fisheries:										
Columbia River.....	Sport.....	2	15,584	----------					46.51	724,812
		3	10,855	----------					49.63	538,734
Zones 1-5 & 7.....	Commercial...	2	2,580	--[6]	3.6	1.6	9,288	4,128	0.28	2,601
		3	145,242	329	8.7	4.0	1,263,605	580,968	0.35	442,262
Indian fisheries[4].....	Commercial...	2	508	--[6]	3.6	1.6	1,829	813	0.24	439
		3	6,134	--[7]	8.7	4.0	53,366	24,536	0.29	15,476
Subtotal.....	Sport.....	2&3	26,439	----------					-----	1,263,546
	Commercial...	2&3	154,464	----------			1,328,088	610,445	-----	460,778
Total.....	All fisheries		1,050,190	----------					-----	9,065,579

1/ Weights for ocean commercial fisheries are dressed weights and those for Columbia River fisheries are round weights. Original weights are in pounds for Ad marked fish.
2/ Entries for Washington and Columbia River fisheries (dollars per pound) were obtained from Dale Ward, Washington State Department of Fisheries (personal communication). Washington price was used for British Columbia and Oregon commercial fisheries. Entry for California was obtained from Pat O'Brien, California Department of Fish and Game (personal communication).
3/ The value of a sport caught coho is based on a value of $20.00 per angler day divided by the catch per angler.
4/ Columbia River set net and dip net fisheries and Klickitat River dip net fishery.
5/ No sampling for weight was done in the Washington commercial fisheries. Average weight obtained from Sam Wright, Washington Department of Fisheries (personal communication).
6/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight obtained from Paul Hirose, Fish Commission of Oregon (personal communication).
7/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight from zones 1-5 used.

in estimates comparable to those originally reported for the 1962 Oregon survey (Gordon, n.d.).[8]

The value of $20 per day is believed to be a reasonable estimate based on existing research information. However, limitations associated with this estimated value should be recognized. A range of values is needed for sport-caught fish that reflect differences in quality variables such as distance from metropolitan areas, environmental conditions, species involved, and success level. The reports mentioned here not only indicate an average value for these different variables but involve different time periods, geographic areas, and research methods. This is also an estimated market value and does not include other values such as consumer surplus (i.e., benefits to consumers that are not measured by market prices), benefits due to employment and income generated in local communities and the regional and national economy, and benefits to nonusers who may not fish but may want fishing preserved and available.

Since the value per fishing day is an average of various quality factors, no values by species are estimated directly. The only method presently available to determine values for fish is by success levels. This requires careful interpretations; for example, greater success results in lower values per fish. This means that higher total values would result with poorer success since the number of fish involved at the estimated market price is not fully taken into account. For this report, success is assumed to be estimated at an average of the total landings of all species. This is probably reasonable since mostly ocean fishing and entire seasons are involved.

Limitations of estimated sport and commercial values need to be emphasized. The estimated market price of $20 per fishing day excludes consumer surplus whereas the estimated number of fishing days does not. Consequently, multiplying market prices by actual participation is not comparable with the ex-vessel prices used for values of commercially caught fish since these values do not contain consumer surplus. Therefore extreme caution should be observed in comparing values between fish species or total values of sport and commercial fishing.

[8] Douglas Gordon. (n.d.). An economic analysis of Idaho sport fisheries. Univ. Idaho, Coll. Forestry, Wildl. and Range Sci., Idaho Coop. Fish. Unit., Review draft, 60 p. (Processed.)

To obtain values for the 1965- and 1966-brood sport-caught coho salmon, the estimated market value of $20 per day of fishing is divided by the success level in each region. This value per fish is then multiplied by the number of coho taken in each region. The results are presented in Tables 8a and 8b.

Benefit/Cost

The total net economic values of the 1965- and 1966-brood coho salmon were $8,508,590 and $9,065,579, respectively. Benefits were also derived from the sale of excess 1965- and 1966-brood coho carcasses at the study hatcheries. The revenue from carcass sales is used to purchase additional fish food. This allows additional fish to be reared, thus providing future benefits to society.

Coho carcasses were sold at Fish Commission of Oregon and Washington Department of Fisheries hatcheries. The values of the 1965- and 1966-brood coho carcasses sold are $75,035 and $40,973, respectively. When these values are added to the net economic values, total benefits of $8,583,625 for the 1965 brood and $9,106,552 for the 1966 brood are obtained. The benefit to cost ratios are then $8,583,625/$1,292,300 or 6.6/1 and $9,106,552/$1,226,600 or 7.4/1 for the 1965 and 1966 broods, respectively. The average benefit to cost ratio is 7.0/1.

SUMMARY

When this marking study was designed, four marks were available from the Pacific Marine Fisheries Commission. The Columbia River was divided into four sections. Each section was assigned a specific mark. All study hatcheries within a given section (except Leavenworth station in the Uppermost River section) marked approximately 10% of their coho salmon production with the assigned mark (Table 2). Two broods, 1965 and 1966, of coho salmon were included in the study. During the 2-year marking phase, 4.1 million of the 40.1 million total coho production were marked (Table 2). Approximately 22.9 million 1965-brood and 17.2 million 1966-brood coho were released (Table 2).

Sampling for marks was conducted in most coho salmon fisheries, with few exceptions, from Avila Beach, Calif., to Pelican, Alaska (Figure

2 and Table 3). During 1968 and 1969, there was no sampling done in the southeast Alaska troll and gillnet fisheries. During the 3 yr of mark sampling, an average of 15.4% of the coho catch was examined for marks (Table 4). A total of 37,632 marked coho was recovered from 1967 through 1969 (Tables 5a and 5b).

The appropriateness of the estimating procedures used to determine hatchery contribution is dependent on the validity of six assumptions. Additional studies and data collections previously described were incorporated into the marking experiment to help test the assumptions. The first assumption, permanence of fin marks, was tested by holding marked fish in fresh water over a period of months. Little total regeneration occurred, but maxillary regeneration caused confusion between maxillary-adipose and adipose-only marked coho salmon. The second assumption, origin of fish marked with hatchery marks, was tested by examining returning adult coho prior to the marking study and coho fingerlings at the time of marking for natural marks. No noteworthy numbers of naturally missing adipose fins or maxillary bones were observed. Prior to this study, a number of age studies have supported that Assumption 3, all adult coho are 3 yr old, is valid (Godfrey, 1965). The mark sampling data (Appendix Tables 2a and 2b) indicate that the fourth assumption, same maturity schedule for marked and unmarked fish, is valid. Appendix Tables 1a and 1b show the validity of Assumption 5, hatcheries in a given section have the same proportion of marked releases. Assumption 6, equality of ocean distribution could not be tested because regeneration and nondetection of maxillary marks distorted the picture.

A total of 179,096 marked 1965- and 1966-brood coho salmon were estimated to have been caught. An additional 33,910 marked coho returned to study hatcheries to spawn (Tables 6a and 6b). The theoretical estimated catch assuming no marking had taken place was 2,188,172 coho and comprised about 16.1% of the total catch of 1965-66 brood coho in the fisheries sampled (Table 7).

The estimated costs of rearing the 1965 and 1966 broods of coho salmon are $1,292,300 and $1,226,600, respectively. The estimated benefits, including carcass sales, received from the harvest of these two broods of coho are $8,583,625 and $9,106,552, respectively. The benefit to cost ratios are then 6.6 to 1 for the 1965 brood and 7.4 to 1 for the 1966 brood.

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APPENDIX TABLE 1a.—Estimated numbers, percent marked, and mean weights of 1965-brood coho salmon released from study hatcheries.

Hatchery group and (in parentheses) mark	Number of fish			Percent marked	Mean weight[1]
	Marked	Unmarked	Total		
Lower River (Ad-RM)					
Elokomin	118,137	1,170,725	1,288,862	0.0917	14
Big Creek	164,759	1,363,618	1,528,377	0.1078	29
Grays River	106,986	946,441	1,053,427	0.1016	23
Klaskanine	118,412	1,190,010	1,308,422	0.0905	33
Total Ad-RM	508,294	4,670,794	5,179,088	0.0981	25
Middle River (Ad)					
Bonneville	81,402	786,425	867,827	0.0938	22
Washougal	245,489	2,152,336	2,397,825	0.1024	24
Sandy	85,871	868,250	954,121	0.0900	27
Eagle Creek[2]	69,988	610,113	680,101	0.1029	16
Lewis[3]	65,453	649,490	714,943	0.0915	28
Kalama Falls	148,242	1,434,022	1,582,264	0.0937	27
Lower Kalama	37,069	315,463	352,532	0.1052	27
Toutle	112,160	1,079,261	1,191,421	0.0941	25
Total Ad	845,674	7,895,360	8,741,034	0.0967	19
Upper River (Ad-LM)					
Klickitat	146,123	1,365,134	1,511,257	0.0967	16
Little White Salmon[4]	357,407	3,290,348	3,647,755	0.0980	15
Willard	--	--	--	--	19
Carson	158,868	1,477,931	1,636,799	0.0971	15
OxBow[5]	47,578	424,892	472,470	0.1007	29
Cascade	127,853	1,112,234	1,240,087	0.1031	26
Total Ad-LM	837,829	7,670,539	8,508,368	0.0985	19
Uppermost River (D-Ad)					
Leavenworth	101,734	402,272	504,006	0.2018	25
TOTAL ALL HATCHERIES	2,293,531	20,638,965	22,932,496	0.1000	--

1/ Mean weights in grams per fish. Values in total lines are averages weighted by total release at each hatchery in that river section.
2/ Additional 70,198 fish released with LM mark.
3/ Includes release from Speelyai hatchery.
4/ Includes release from Willard hatchery.
5/ Released from Bonneville hatchery.

APPENDIX TABLE 1b.—Estimated numbers, percent marked, and mean weights of 1966-brood coho salmon released from study hatcheries.

Hatchery group and (in parentheses) mark	Number of fish			Percent marked	Mean weight[1]
	Marked	Unmarked	Total		
Lower River (Ad-RM)					
Elokomin	85,319	761,349	846,668	0.1008	28
Big Creek	122,552	1,159,780	1,282,332	0.0956	23
Grays River	60,852	530,173	591,025	0.1030	27
Klaskanine	116,907	1,118,505	1,235,412	0.0946	28
Total Ad-RM	385,630	3,569,807	3,955,437	0.0975	26
Middle River (Ad)					
Bonneville	146,457	1,361,388	1,507,845	0.0971	24
Washougal	85,741	769,789	855,530	0.1002	25
Sandy	98,702	920,106	1,018,808	0.0969	22
Eagle Creek[2]	130,384	1,028,499	1,158,883	0.1125	20
Lewis[3]	85,442	882,958	968,400	0.0882	27
Kalama Falls	85,022	789,515	874,537	0.0972	28
Lower Kalama	38,792	357,123	395,915	0.0980	27
Toutle	93,722	856,325	950,047	0.0986	24
Total Ad	764,262	6,965,703	7,729,965	0.0989	24
Upper River (Ad-LM)					
Klickitat	79,864	770,023	849,887	0.0940	28
Little White Salmon[4]	369,935	3,339,807	3,709,742	0.0997	20
Willard	--	--	--	--	17
Carson[5]	--	--	--	--	--
OxBow[5]	--	--	--	--	--
Cascade	43,311	434,846	478,157	0.0905	23
Total Ad-LM	493,110	4,544,676	5,037,786	0.0979	20
Uppermost River (D-Ad-RM, D-Ad-LM[6])					
Leavenworth	78,092	269,355	347,447	0.2248	23
Leavenworth[6]	96,643	466	97,109	0.9952	23
TOTAL ALL HATCHERIES	1,817,737	15,350,007	17,167,744	0.1059	--

1/ Mean weights in grams per fish. Values in total lines are averages weighted by total release at each hatchery in that river section.
2/ Additional 126,323 fish released with LM mark, 87,733 released with An mark, and 127,514 released with RM mark.
3/ Includes release from Speelyai hatchery.
4/ Includes releases from Willard hatchery.
5/ Nonparticipating for 1966 brood.
6/ Released below Bonneville Dam.

APPENDIX TABLE 2a.—Number of marked and unmarked 1965-brood coho salmon recovered at hatcheries in each section of the Columbia River in 1967 and 1968.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1967	1968
Middle River--Continued				
Lewis River	Unmarked	--	1,072	1,894
	Ad-LM	Upper river	0	0
	Ad	Lewis	88	235
	Ad-RM	Lower river	0	0
Kalama Falls	Unmarked	--	1,176	10,451
	Ad-LM	Upper river	0	0
	Ad	Kalama Falls	107	865
	Ad-RM	Lower river	0	0
Lower Kalama	Unmarked	--	524	1,915
	Ad-LM	Upper river	0	0
	Ad	Lower Kalama	89	227
	Ad-RM	Lower river	0	0
Toutle	Unmarked	--	4,417	24,931
	Ad-LM	Upper river	0	0
	Ad	Toutle	416	2,030
	Ad-RM	Lower river	0	0
Upper River				
Klickitat	Unmarked	--	916	1,398
	Ad-LM	Klickitat	41	117
	Ad	Mid river	6	27
	Ad-RM	Lower river	0	0
Little White Salmon	Unmarked	--	1,044	5,403
	Ad-LM	Little White Salmon	46	419
	Ad	Mid river	8	58
	Ad-RM	Lower river	0	0
OxBow	Unmarked	--	(*)	103
	Ad-LM	OxBow	(*)	3
	Ad	Mid river	(*)	2
Cascade	Unmarked	--	7,247	7,227
	Ad-LM	Cascade	549	576
	Ad	Mid river	44	104
	Ad-RM	Lower river	5	21
Uppermost River				
Leavenworth	Unmarked	--	310	1,849
	D-Ad	Leavenworth	38	138

*Returns not examined.

APPENDIX TABLE 2a.—Continued.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1968	1969
Middle River--Continued				
Lewis River	Unmarked	--	1,911	2,945
	Ad-LM	Upper river	0	0
	Ad	Lewis River	233	302
	Ad-RM	Lower river	0	0
Kalama Falls	Unmarked	--	1,592	10,696
	Ad-LM	Upper river	0	0
	Ad	Kalama Falls	148	888
	Ad-RM	Lower river	0	1
Lower Kalama	Unmarked	--	1,887	2,739
	Ad-LM	Upper river	0	1
	Ad	Lower Kalama	192	263
	Ad-RM	Lower river	0	1
Toutle	Unmarked	--	2,546	23,664
	Ad-LM	Upper river	0	0
	Ad	Toutle	200	2,093
	Ad-RM	Lower river	0	0
Upper River				
Klickitat	Unmarked	--	181	1,347
	Ad-LM	Klickitat	15	163
	Ad	Mid river	2	13
	Ad-RM	Lower river	0	0
Little White Salmon	Unmarked	--	5,036	8,131
	Ad-LM	Little White Salmon	341	666
	Ad	Mid river	44	105
	Ad-RM	Lower river	1	2
Cascade	Unmarked	--	2,144	1,374
	Ad-LM	Cascade	146	83
	Ad	Mid river	41	22
	Ad-RM	Lower river	3	14
Uppermost River				
Leavenworth	Unmarked	--	69	32
	D-Ad	Leavenworth	1	0
	D-Ad-LM	Leavenworth	7	0
	D-Ad-RM	Leavenworth	0	0

APPENDIX TABLE 2b.—Number of marked and unmarked 1966-brood coho salmon recovered at hatcheries in each section of the Columbia River in 1968 and 1969.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1968	1969
wer River				
Elokomin	Unmarked	--	4,527	6,316
	Ad-LM	Upper river	3	1
	Ad	Mid river	2	10
	Ad-RM	Elokomin	280	532
Big Creek	Unmarked	--	5,682	7,719
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	5
	Ad-RM	Big Creek	430	489
Grays River	Unmarked	--	5,375	5,310
	Ad-LM	Upper river	0	2
	Ad	Mid river	0	10
	Ad-RM	Grays River	518	516
Klaskanine	Unmarked	--	10,473	2,623
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	0
	Ad-RM	Klaskanine	788	172
ddle River				
Bonneville	Unmarked	--	7,034	3,115
	Ad-LM	OxBow	90	148
	Ad	Bonneville	585	567
	Ad-RM	Lower river	26	24
Washougal	Unmarked	--	2,204	9,060
	Ad-LM	Upper river	0	0
	Ad	Washougal	237	1,033
	Ad-RM	Lower river	0	7
Sandy	Unmarked	--	4,134	3,079
	Ad-LM	Upper river	27	11
	Ad	Sandy	422	267
	Ad-RM	Lower river	20	13
Eagle Creek	Unmarked	--	929	1,799
	Ad-LM	Upper river	2	0
	Ad	Eagle Creek	85	191
	Ad-RM	Lower river	1	0
	LM	Eagle Creek	77	221

APPENDIX TABLE 2b.—Continued.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1967	1968
ower River				
Elokomin	Unmarked	--	533	1,616
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	3
	Ad-RM	Elokomin	41	105
Big Creek	Unmarked	--	10,540	10,573
	Ad-LM	Upper river	0	0
	Ad	Mid river	26	5
	Ad-RM	Big Creek	936	1,079
Grays River	Unmarked	--	1,363	2,651
	Ad-LM	Upper river	3	0
	Ad	Mid river	41	0
	Ad-RM	Grays River	40	213
Klaskanine	Unmarked	--	7,201	4,151
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	1
	Ad-RM	Klaskanine	527	365
iddle River				
Bonneville	Unmarked	--	7,401	16,602
	Ad-LM	OxBow	468	735
	Ad	Bonneville	188	787
	Ad-RM	Lower river	5	44
Washougal	Unmarked	--	22,098	43,264
	Ad-LM	Upper river	0	3
	Ad	Washougal	2,651	4,316
	Ad-RM	Lower river	0	3
Sandy	Unmarked	--	6,021	5,222
	Ad-LM	Upper river	18	24
	Ad	Sandy	664	517
	Ad-RM	Lower river	14	32
Eagle Creek	Unmarked	--	593	2,371
	Ad-LM	Upper river	0	5
	Ad	Eagle Creek	63	222
	Ad-RM	Lower river	0	2
	LM	Eagle Creek	58	215

APPENDIX TABLE 3.—Percentage of two-year-old coho salmon in the marked and unmarked returns to Columbia River hatcheries by river section and brood year, 1965-66.

River section and (in parentheses) mark	Brood	Percent of 2-year-olds	
		Marked	Unmarked
Lower (Ad-RM)	1965	47	51
	1966	54	54
Middle (Ad)	1965	32	29
	1966	27	28
Upper (Ad-LM)	1965	36	40
	1966	36	40

APPENDIX TABLE 4.—Actual number of marked coho salmon of the 1966 brood from Leavenworth National Fish Hatchery recovered—by type of mark, year of recovery, region of capture, and type of fishery, 1968-69.

Region	Fishery type	D-Ad		D-Ad-RM		D-Ad-LM[1/]		Total	
		1968	1969	1968	1969	1968	1969	1968	1969
British Columbia.....	Commercial.....	0	0	0	0	0	1	0	1
Washington.....	Sport.....	0	18	0	5	0	29	0	52
	Commercial.....	0	30	0	7	0	30	0	67
Oregon.....	Sport.....	0	20	0	5	0	6	0	31
	Commercial.....	0	34	0	32	0	52	0	118
California.....	Sport.....	0	2	0	1	0	3	0	6
	Commercial.....	0	19	0	8	0	13	0	40
Columbia River.....	Sport.....	0	0	0	0	0	0	0	0
	Commercial.....	3	2	0	15	0	33	3	50
Total.....	All fisheries..	3	125	0	73	0	167	3	365

1/ Released below Bonneville Dam.

APPENDIX TABLE 5a.—Estimated number of marked coho salmon of the 1966 brood from Leavenworth National Fish Hatchery recovered—by type of mark, year of recovery, region of capture, and type of fishery, 1968-69.

Region	Fishery type	D-Ad		D-Ad-RM		D-Ad-LM[1]		Total	
		1968	1969	1968	1969	1968	1969	1968	1969
British Columbia.....	Commercial.....	0	0	0	0	0	7	0	7
Washington.....	Sport.....	0	88	0	23	0	131	0	242
	Commercial.....	0	123	0	30	0	128	0	281
Oregon.....	Sport.....	0	114	0	15	0	19	0	148
	Commercial.....	0	184	0	176	0	285	0	645
California.....	Sport.....	0	7	0	2	0	14	0	23
	Commercial.....	0	137	0	35	0	52	0	224
Columbia River.....	Sport.....	0	0	0	0	0	0	0	0
	Commercial.....	6	7	0	90	0	186	6	283
Total.....	All fisheries..	6	660	0	371	0	822	6	1,853

1/ Released below Bonneville Dam.

APPENDIX TABLE 5b.—Estimated recovery of D-Ad-RM and D-Ad-LM marked 1966-brood coho salmon from Leavenworth National Fish Hatchery after redistribution of the D-Ad-only marks.

Region	Fishery type	D-Ad-RM		D-Ad-LM[1]		Total	
		1968	1969	1968	1969	1968	1969
British Columbia.....	Commercial.....	0	0	0	7	0	7
Washington.....	Sport.....	0	71	0	171	0	242
	Commercial.....	0	96	0	185	0	281
Oregon.....	Sport.....	0	77	0	71	0	148
	Commercial.....	0	275	0	370	0	645
California.....	Sport.....	0	6	0	17	0	23
	Commercial.....	0	109	0	115	0	224
Columbia River.....	Sport.....	0	0	0	0	0	0
	Commercial.....	3	94	3	189	6	283
Total.....	All fisheries..	3	728	3	1,125	6	1,853

1/ Released below Bonneville Dam.

APPENDIX TABLE 6.—Relative survival of marked 1965- and 1966-brood coho salmon by mark type and hatchery groups.

Brood	Mark	Tetracycline group	Cascade, Little White, Klaskanine	All hatcheries
1965	Ad-LM	--	.69[3/]	.69[5/]
	Ad	.89[1/]	--	.92[6/]
	Ad-RM	.82[2/]	.79[4/]	.79
1966	Ad-LM	--	.68[3/]	.72
	Ad	.83[1/]	--	.89[6/]
	Ad-RM	.68[2/]	.70[4/]	.72

1/ Eagle Creek National Fish Hatchery.
2/ Big Creek Salmon Hatchery.
3/ Cascade Salmon Hatchery, Little White Salmon National Fish Hatchery.
4/ Klaskanine River Salmon Hatchery.
5/ Klickitat State Salmon Hatchery, Cascade Salmon Hatchery, Little White Salmon National Fish Hatchery.
6/ Bonneville Salmon Hatchery returns not included in calculations.

APPENDIX TABLE 7.—Estimated catch of unmarked 1965- and 1966-brood hatchery coho salmon by region, fishery type, brood year, and year of capture.

Region	Fishery type	1965 brood			1966 brood		
		1967	1968	Total	1968	1969	Total
Ocean fisheries:							
British Columbia.....	Commercial...	0	80,101	80,101	0	34,981	34,981
Washington.....	Sport.....	0	163,997	163,997	0	153,837	153,837
	Commercial...	0	203,620	203,620	0	122,210	122,210
Oregon.....	Sport.....	0	93,759	93,759	0	86,658	86,658
	Commercial...	0	270,127	270,127	0	298,453	298,453
California.....	Sport.....	0	7,878	7,878	0	7,529	7,529
	Commercial...	0	102,523	102,523	0	77,724	77,724
Subtotal.....	Sport.....	0	265,634	265,634	0	248,024	248,024
	Commercial...	0	656,371	656,371	0	533,368	533,368
Freshwater fisheries:							
Columbia River.....	Sport.....	3,928	3,246	7,174	6,516	4,771	11,287
	Commercial...	1,733	74,548	76,281	2,775	136,057	138,832
Total.....	All fisheries	5,661	999,799	1,005,460	9,291	922,220	931,511

APPENDIX TABLE 8.—Estimated total catch of 1965- and 1966-brood hatchery coho salmon by region, fishery type, brood year, and year of capture.

Region	Fishery type	1965 brood			1966 brood		
		1967	1968	Total	1968	1969	Total
Ocean fisheries:							
British Columbia.....	Commercial...	0	87,526	87,526	0	38,313	38,313
Washington.....	Sport.....	0	179,179	179,179	0	167,914	167,914
	Commercial...	0	222,405	222,405	0	133,536	133,536
Oregon.....	Sport.....	0	102,614	102,614	0	94,994	94,994
	Commercial...	0	294,778	294,778	0	326,241	326,241
California.....	Sport.....	0	8,556	8,556	0	8,259	8,259
	Commercial...	0	111,592	111,592	0	85,165	85,165
Subtotal.....	Sport.....	0	290,349	290,349	0	271,167	271,167
	Commercial...	0	716,301	716,301	0	583,255	583,255
Freshwater fisheries:							
Columbia River.....	Sport.....	4,297	3,552	7,849	7,133	5,223	12,356
	Commercial...	1,872	81,364	83,236	3,021	148,533	151,554
Total.....	All fisheries	6,169	1,091,566	1,097,735	10,154	1,008,178	1,018,332

APPENDIX TABLE 9.—Estimated 1967-69 sport catch in Columbia River tributaries (where no creel census was made) of 1965- and 1966-brood hatchery coho salmon.

Stream	1965 brood			1966 brood			Estimation method
	1967	1968	Total	1968	1969	Total	
Icicle River	50	15	65	10	10	20	1/
Klickitat River	5	6	11	5	0	5	2/ 3/ 4/
Little White Salmon R.	111	8	119	7	2	9	2/ 3/ 5/
Wind River	2	0	2	--	--	--	2/ 3/ 4/
Washougal River (upper)	10,382	2,048	12,430	2,493	872	3,365	1/ 3/ 5/
(lower)	1,385	273	1,658	332	116	448	1/ 3/ 4/
Elokomin River	59	75	134	92	115	207	2/ 3/ 4/
Grays River	10	218	228	265	213	478	2/ 3/ 4/
Sandy River	513	944	1,457	1,457	1,198	2,655	3/ 4/ 6/
Eagle Creek (Clackamas)	928	1,709	2,637	1,744	1,433	3,177	3/ 4/ 6/
Big Creek	410	754	1,164	603	496	1,099	3/ 4/ 6/
Klaskanine River	534	983	1,517	1,346	1,106	2,452	3/ 5/ 6/
TOTAL	14,389	7,033	21,422	8,354	5,561	13,915	

1/ Estimates from discussions with Gene Nye, Washington Department of Fisheries, and local fishery personnel.
2/ Catches from Washington Department of Fisheries punch card returns 1967-1969.
3/ Age groups broken down by using jack to adult ratios obtained in creel census on Lewis, Kalama, Cowlitz, and Toutle Rivers.
4/ 70% of catch apportioned to hatchery production.
5/ Entire catch assumed hatchery.
6/ Catches from Oregon State Game Commission punch card returns 1967-1969.

ABILITY OF MALE KING CRAB, *PARALITHODES CAMTSCHATICA*, TO MATE REPEATEDLY, KODIAK, ALASKA, 1973

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ABSTRACT

An experiment to test abilities of male king crab to mate repeatedly in an environment approximating natural conditions was conducted during the spring of 1970. Twenty-four males of varying size and shell age were placed into separate undersea compartments for intervals up to 56 days with 222 females. The ability of males to mate repeatedly was determined by introducing females in mating condition to males at the rate of one every 5 days.

No difference in mating capabilities of males of different types was evident until after exposure to seven females. At this point egg fertility and relative fullness of brood chamber of the females mated to the small old-shell males decreased significantly. Large new-shell males showed a marked decline in mating ability after the ninth mating. One small new-shell male mated with 13 females.

Owing to declining stocks within the Kodiak Island fishery, commercial harvest of king crab has declined from 96 to 11 million pounds over the past seven years, 1965-1971. To determine the level of king crab brood stocks necessary for perpetuation of a maximum sustained yield fishery, the reproductive capabilities of the king crab are being studied in detail.

In 1964, biologists of the Alaska Department of Fish & Game determined experimentally that recently-molted sublegal (smaller than 146 mm carapace length) male king crabs were capable of mating. Eleven males ranging from 120 to 144 mm carapace length mated 51 females in 16 days (Powell and Nickerson, 1965). Observations on individual males were not obtained. In 1971, males as small as 85 mm carapace length were found to be capable of mating (Powell, Shafford, and Jones, 1972). Of 3,402 males observed mating in nature from 1963 to 1971, however, only two were smaller than 100 mm (Powell, Rothschild, and Buss[4]).

Several authors have reported old-shell males congregated with adult females during the mating season and indicated they may be capable breeders because new-shell males were separate from the females at the time (Gray and Powell, 1966; Miyahara and Shippen, 1965).

Currently the reproductive success or failure of any particular brood year is not readily apparent until approximately 8 yr later when males are entering the fishery. At this late date, it is doubtful that we can, with any precision, evaluate the degree to which each of the limiting factors contributes to the success or failure; consequently we are unable to determine if resultant abundance levels are attributable to initial magnitude of egg production, environment, or effects of commercial fishing.

Prior to 1970, managers assumed that any level of harvest of males was acceptable as long as the 7-inch size limit (carapace width outside spines) was observed.

In recent years, we observed that the proportion of adult females without eggs and with partial broods had increased and that some of the female population was not being serviced (unpublished Alaska Department of Fish & Game data). Large adult females have approximately nine times more eggs than small ones (Haynes, 1968) and initial examination of unpublished Department of Fish & Game data reveals that the incidence of adults without eggs and with partial broods is greater among the

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[4] Powell, Guy C., Brian J. Rothschild, and James A. Buss. 1972. A study of king, *Paralithodes camtshatica* (Tilesius) brook stocks, Kodiak Island, Alaska, 1963-1971. 30 p. (Processed)

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larger individuals. In order to place more males on the mating grounds and to stabilize annual harvests, a quota system was initiated in 1970.

It is important to know whether that segment of the male population harvested by the commercial fishery, i.e., large males and old-shell males (Nickerson, Ossiander, and Powell, 1966) possess greater mating capabilities than smaller protected males which molt during the mating season. Also of significance is the question of whether undersized males would be adequate in numbers and ability to mate all females if larger males were removed by the fishery. Recent increases in the numbers of adult females with broods of reduced size appear related to simultaneous increased exploitation rates and may result from matings with males which had mated several times previously. Our experiment was designed to gain insight into these phenomena and to obtain more complete data for individual males, especially comparative data on mating ability for old-shell males and recently molted new-shell males.

In this paper, mating refers to the actual fertilization of the eggs. Hence, the term "mating capability" refers to the ability of the male to fertilize the eggs of the females to which he is exposed.

METHODS AND MATERIALS

Experimental Equipment and Location

The experiment was conducted in undersea pens, the sides and top of which were covered with nylon mesh; the bottoms were open to allow crabs to dig in the substrate as they would do in nature. Each pen was $8' \times 8' \times 4'$ and each divided into four equal sized compartments. Compartments were numbered 1 through 28 and situated in 40 ft of water on a level stretch of muddy-sand bottom east of Near Island adjacent to an area where king crabs normally mate. The study location is one mile from the city of Kodiak, Alaska. Pens were designed and located to simulate natural conditions. Environmental factors such as daily tidal currents, pressures, light intensities, temperatures, and salinities were considered important in that they might influence mating. For this reason, undersea pens were considered superior to aquaria.

The mating study was conducted in compartments 1 through 24 while 25 through 28 were used to store crabs. Females were held in storage prior to and after the completion of mating.

Fishery biologists and trained technicians utilizing scuba observed the crabs underwater every day. Individual crabs were identified by tagging with permanent "isthmus" loop tags (Gray, 1965) prior to being placed in the pens.

Experimental Procedures

The experiment was designed to compare mating capabilities of four size shell-age classes of male king crabs (small new-shell, small old-shell, large new-shell, and large old-shell) by studying the effects of repeated matings on the ability of these males to mate successfully with additional females. A 5-mm range, 145-149, was used as a dividing point between small and large males at the juncture of legal and undersize crabs. Those 144 mm or less (commercially undersize males) were classified as small while those 150 mm or larger were classified as large (Table 1). Small males averaged 140 mm, large males 167.

Most males used in the experiment were captured by scuba divers. A few of the males of required size, however, were not available by diving (the preferred method of collecting) and therefore were taken from the catches of commercial pots and trawls.

All females used in the study were in premolt condition and were in the pre-copulatory embrace (Powell and Nickerson, 1965): i.e., they had already been selected for mating by males in the natural environment. The use of these females (called "graspees") was our method of insuring that females were ready to mate with males when introduced into the pens. Females from natural mating areas near the pens were captured by scuba divers a day or two before they were needed and ranged in length from 104 to 181 mm, with an average size of 134 mm.

TABLE 1.—Size relationships of experimental crabs.

Male king crabs		No. of female partners	Carapace length (mm)			
			Range		Mean	
Class	Number		Male	Female	Male	Female
Small old-shell	4	29	136-144	107-181	142	133
Large old-shell	9	82	156-193	114-175	178	134
Small new-shell	4	35	136-142	115-150	139	135
Large new-shell	10	76	150-168	104-160	158	134
Total	27[1]	222				

[1] Three extra males replaced three original males which died.

Females were separated from the males which held them and placed in storage ready for use in the experiment. The average length of females increased as the study progressed because older females mate later in the season.[5] Females captured 15 March through 15 April averaged 128 mm, while those captured 20 April to 20 May averaged 140.

Twenty-four females were paired randomly with the 24 males in the pens at the beginning of each of the 14 separate 5-day periods beginning 16 March and continuing through 24 May. On days when a complete set of 24 females could not be captured, those which had been were introduced to males which previously had had the largest number of female partners. Incomplete sets of females exist for early and late spawning periods—1, 2, 3, 12, 13, and 14—when mating crabs were relatively scarce. In addition, 12 females escaped from six compartments on 9 May when two pens were accidentally lifted; as many as three females were lost from a single compartment. During the middle of the mating season, 31 March through 5 May, females were abundant; consequently each male received a female for each of the eight consecutive periods within this interval. Females were introduced to males as soon after capture as possible; none were held more than two days and many were introduced the same day.

Females were left with males until mating was completed and eggs were known to be fertilized; consequently males commonly shared their compartments with several females at a time. Approximately 10 days after eggs were deposited on the pleopods, a sample of approximately 1,000 was obtained from each female to determine success of fertilization. Each sample consisted of several separate groups of eggs taken from scattered locations within the egg mass. Samples were preserved in Bouin's solution. Fertilized eggs developing for 7 to 10 days at approximately 37°F showed cleavage when viewed microscopically. When eggs were known to be fertilized (i.e., advanced cleavage stages observed), females were separated from their experimental male partners and placed in storage compartments 25-28.

Divers made observations at daily intervals recording data on underwater slates. Observations included collecting and measuring shed exoskeletons to determine day of molting, examining recently-molted females to determine relative fullness of the brood chamber, and recording activities of mating and feeding.

RESULTS

Relative success of male copulation was measured in two ways. First, relative fullness of brood chamber was determined subjectively by visually deciding what proportion of the brood chamber was filled with eggs and recording same on a scale of zero to one hundred (Table 2). The second, percent of eggs fertilized, was determined in two steps; (1) a prompt microscopic viewing of several hundred eggs to obtain quick estimates, followed later by (2) a careful microscopic examination of 100 eggs (Table 3).

Both measures of mating success provided compatible results and revealed that infertile eggs are scattered throughout the egg mass rather than being grouped separately from fertile eggs.

The raw data, y, for each of the two measurement variables were transformed so that they would be more normally distributed, using the formula:[6]

$$z = \sqrt{n + 1/2} \sin \sqrt[-1]{\frac{y + 3/8^*}{n + 3/4}}$$

In this case, n is equal to 100, since both methods of measurement are based on a scale of 100.

A covariance analysis was performed relating z to x, the number of females mated. This analysis fits a least squares regression line $z = a_i + b_i x$ for each of the four groups, where a_i, b_i represent the intercept and slope respectively for the ith group. The results of this analysis are presented in Table 4. Slopes for each group appear to be significantly different from zero, except for percent of eggs fertilized in large old-shell and small new-shell males. The more negative the slope of the regression line, the less the

[5] Determined from 3,402 observations of grasping pairs of king crabs captured over a 9-year period, 1963-1971. See page 257 National Geographic Magazine, Vol. 139, No. 2, Feb. 1971 for photograph of grasping pairs.

[6] Thoni, H. Transformation of variables used in the analysis of experimental and observational data, a review. Technical Report No. 7, Statistical Laboratory, Iowa State University, Ames, Iowa, July 1967.

TABLE 2.—Success of each mating as determined by the relative fullness of the brood chamber (percent).

Male class	Male carapace length (mm)	Number of successive matings: Relative fullness of brood chamber (percent)													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Small old-shell	144	100	100	100	90	—	—	—	—	—					
	136	100	100	100	0	80	80	50	0	0					
	144	100	100	100	100	80	85	60	50	0					
	142	100	90	90	10	85	90	100	—	—					
No. of observations	4	4	4	4	4	3	3	3	2	2					
Average	141.5	100	97.5	97.5	50	81.7	85.0	70.0	25.0	0					
Large old-shell	164	100	100	90	100	80	90	80	75	80					
	156	80	100	90	100	100	100	90	20	80	30	—	—	—	—
	163	100	90	100	100	100	100	—	—	—	—	—	—	—	—
	190	100	100	100	100	90	100	100	90	90	75	80	90	5	35
	184	100	100	70	100	100	90	90	100	—	—	—	—	—	—
	193	100	90	95	100	50	100	90	60	80	0	—	—	—	—
	181	100	85	100	100	90	100	100	—	—	—	—	—	—	—
	180	100	100	100	100	100	100	90	75	20	85	—	—	—	—
	189	90	90	100	90	90	75	20	90	—	—	—	—	—	—
No. of observations	9	9	9	9	9	9	9	8	7	5	4	1	1	1	1
Average	177.8	96.7	95.0	93.9	98.9	88.9	95.0	82.5	72.9	70.0	47.5	80	90	5	35
Small new-shell	140	60	100	100	80	100	100	90	100	100	100	60	60	50	—
	136	100	75	80	100	75	60	—	—	—	—	—	—	—	—
	142	100	80	60	90	75	90	50	75	25	—	—	—	—	—
	138	100	100	90	100	100	90	90	—	—	—	—	—	—	—
No. of observations	4	4	4	4	4	4	4	3	2	2	1	1	1	1	
Average	139.0	90	88.8	82.5	92.5	87.5	85.0	76.7	87.5	62.5	100	60	60	50	
Large new-shell	150	75	100	100	100	90	90	—	—	—	—	—	—		
	160	100	100	100	70	100	0	90	90	90	70	0	0		
	165	10	100	100	10	100	75	80	70	90	100	80	—		
	163	100	90	100	100	90	60	90	50	60	—	—	—		
	168	100	90	90	100	100	100	100	10	80	75	—	—		
	161	100	100	100	100	90	75	60	—	—	—	—	—		
	160	100	100	90	80	35	—	—	—	—	—	—	—		
	153	100	—	—	—	—	—	—	—	—	—	—	—		
	151	100	70	70	100	90	90	80	50	60	60	0	—		
	151	100	85	80	100	—	—	—	—	—	—	—	—		
No. of observations	10	10	9	9	9	8	7	6	5	5	4	3	1		
Average	158.2	88.5	92.8	92.2	84.4	86.9	70.0	83.3	54.0	76.0	76.2	26.7	0		

TABLE 3.—Success of each mating as determined by percent of egg mass fertilized.

Male class	Male carapace length (mm)	Number of successive matings													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		Percent of eggs fertilized													
Small old-shell	136	100	100	100	0	97	79	99	0	0					
	142	100	100	100	87	96	90	99	—	—					
	144	100	100	100	100	100	100	82[2]	99[2]	0					
	144	100	100	100	90	—	—	—	—	—					
No. of observations	4	4	4	4	4	3	3	3	2	2					
Average	141.5	100	100	100	69.3	97.7	89.7	93.3	44.5	0					
Large old-shell	164	100	100	90	100	100	100	100	99	100	—	—	—	—	—
	156	100	100	95	100	100	100	99	91	100	92	—	—	—	—
	163	100	99	100	100	100	100	—	—	—	—	—	—	—	—
	190[1]	100	100	100	100	100	97	98	100	100	100	100	100	[1]	[1]
	184	100	100	100	100	99	100	100	100	—	—	—	—	—	—
	193	99	98	97	100	100	100	99	100	100	0	—	—	—	—
	181	98	100	100	100	100	100	99	—	—	—	—	—	—	—
	180	99	99	100	100	100	100	100	100	100	100	—	—	—	—
	189	100	100	100	100	100	100	100	100	—	—	—	—	—	—
No. of obersvations	9	9	9	9	9	9	9	8	7	5	4	1	1	1	1
Average	177.8	99.6	99.6	98.0	100	99.9	99.7	99.4	98.6	100	73	100	100	[1]	[1]
Small new-shell	140	100[2]	100	100	100	100	100	100[2]	100	98[2]	95[2]	100	97	100[2]	—
	136	98	100	91[2]	94[2]	98[2]	86	—	—	—	—	—	—	—	—
	142	100	100	98	99	100	89	100	99[2]	99[2]	—	—	—	—	—
	138	100	100	100	100	100	100	100[2]	—	—	—	—	—	—	—
No. of observations	4	4	4	4	4	4	4	3	2	2	1	1	1	1	
Average	139.0	99.5	100	97.2	98.2	99.5	93.8	100	99.5	98.5	95	100	97	100	
Large new-shell	150	100	100	100	100	100	100	—	—	—	—	—	—		
	160	100	100	100	100	100	0	97	100	100	91	0	0		
	165	100	100	100	100	98	99	87	97	0	99	59	—		
	163	100	100	100	100	100	100	100	98	100	—	—	—		
	168	100	100	38	100	98	94	97	95	100	35	—	—		
	161	100	100	100	100	99	98	100	—	—	—	—	—		
	160	100	99	99	100	95	—	—	—	—	—	—	—		
	153	100	—	—	—	—	—	—	—	—	—	—	—		
	151	100	100	100	100	100	100	100	99	100	100[2]	0	—		
	151	100	98	100	100	—	—	—	—	—	—	—	—		
No. of observations	10	10	9	9	9	8	7	6	5	5	4	3	1		
Average	158.2	100	99.7	93	100	98.8	84.4	96.8	97.8	80.0	81.2	19.7	0		

[1] The last 2 females ovulated but escaped before egg samples were taken.
[2] Female larger than male.

TABLE 4.—Comparison of king crab mating ability, slopes and slope contrasts for relative fullness of brood chamber and percent of eggs fertilized.

Male class	Relative fullness of brood chamber: Slope	Standard deviation of slope	F Value for Test of slope = 0	Percent of eggs fertilized: Slope	Standard deviation of slope	F Value for Test of slope = 0
Small old-shell	b_1 = -1.416	0.234	F = 36.5 $P < .0001$	b_1 = -1.171	0.202	F = 33.5 $P < 0.0001$
Large old-shell	b_2 = -0.616	0.112	F = 30.3 $P < .0005$	b_2 = -0.087	0.107	F = .7 P = .32
Small new-shell	b_3 = -0.328	0.164	F = 3.9 P = .05	b_3 = -0.036	0.142	F = .1 P = .75
Large new-shell	b_4 = -0.677	0.116	F = 33.9 $P < .0001$	b_4 = -0.637	0.100	F = 40.4 $P < .0001$
Test for equality of slopes $b_1 = b_2 = b_3 = b_4$			F = 4.07, P = 0.01			F = 11.74, P = .0001

Slope Contrasts

	Contrast estimate	Standard deviation of estimate	F Value for test of contrast = 0	Contrast estimate	Standard deviation of contrast	F Value for test of contrast = 0
Old-shell vs. new-shell $b_1 + b_2 - b_3 - b_4$	-1.028	0.329	F = 9.80 P = 0.001	-0.585	0.287	F = 4.1 P = 0.04
Large vs. small $b_1 + b_3 - b_2 - b_4$	-0.450	0.329	F = 1.9 P = 0.17	-0.482	0.287	F = 2.8 P = 0.10

mating ability of the males in that particular group. A test of the hypothesis of equality of slopes ($b_1 = b_2 = b_3 = b_4$) yields an F ratio of 4.1 for relative fullness of brood chamber and 11.7 for percent of eggs fertilized, significant at the 1 and 0.01 percent level respectively. In order to determine the significance of the size shell-age classifications, contrasts of old-shell versus new-shell and small versus large were computed as shown in Table 4. These contrasts indicate that the major contribution to the inequality in slopes comes from the difference in shell age. Size did not appear to be a significant factor as is indicated by P values of 0.17 and 0.10 respectively for relative fullness of brood chamber and percent of eggs fertilized. Within the shell-age contrast, the small old-shell males contribute the most in the form of a more negative slope, indicating that these males have much less mating ability than the other three groups.

The data presented thus far give a comparison of the mating abilities of the four size shell-age groups. A linear approximation was assumed for each group and, although this procedure is not exact, it is sufficiently close for comparative purposes. Graphs of the curves for mating ability versus number of matings indicate that small old-shell and large new-shell males have the least linear relationship of the four groups. The points plotted in Figures 1 and 2 are the means of the transformed variables for each successive mating. A point may represent as few as one or as many as ten observations, as shown in Tables 2 and 3. The original 0 to 100 scale is attached to the graphs to make them easier to read; thus after the means are computed, they are transformed back to the original scale.

The slopes of the functions were approximated by computing the means of the transformed measurement variables for each x and fitting empirical curves to the data points. Figures 1 and 2 show the relationship between percent of eggs fertilized and relative fullness of brood chamber respectively and are presented primarily as an aid to fisheries management. The results, however, are quite consistent with those given in Table 4. The graphs show a marked decline in the mating ability of small old-shell males after approximately the seventh mating and a decline in the ability of large new-shell males after the tenth mating. Figure 2 indicates that partial clutches result from mating with small old-shell and large new-shell males which had mated several times previously.

The least squares regression lines for large old-shell males and small new-shell males are also plotted in Figures 1 and 2. These groups show little decrease in mating ability as the number of matings increases, particularly for the percent of eggs fertilized. The slope of the

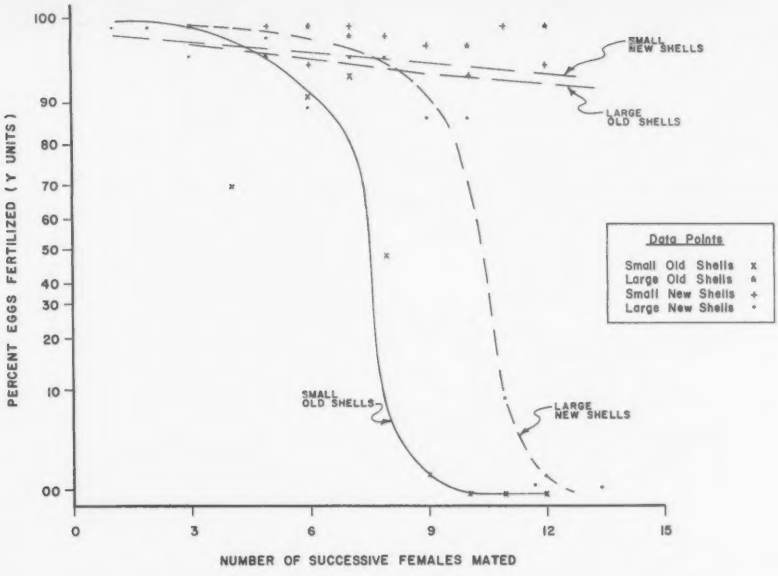

FIGURE 1.—Mating ability of male king crabs expressed as percentage of eggs fertilized.

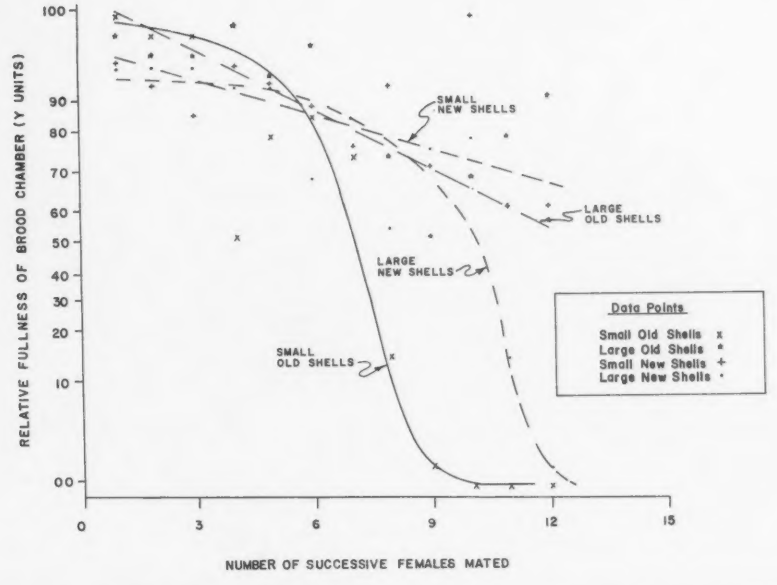

FIGURE 2.—Mating ability of male king crabs expressed as relative fullness of brood chamber of mated females.

regression line for large old-shell males for relative fullness of brood chamber is quite steep (-0.616) and nearly approaches the slope for large new-shell males (-0.677); however, there are no points in the vicinity of zero to indicate that mating ability for large old-shell males drops off suddenly after a certain number of matings. Furthermore, the other measurement variable indicates that the mating ability of large old-shell crabs does not decline at a significant rate when exposed to a maximum of 13 females.

DISCUSSION

This study indicates that all classes of males tested possessed considerable ability to mate repeatedly at the approximate rate of one female every 5 days. Mating ability of small old-shell and large new-shell male king crabs decreases markedly after approximately the seventh to ninth mating. The decline for large old-shells and small new-shells is not as noticeable.

Although the analysis of covariance for this experiment does not indicate significant differences in mating ability attributable to size, one should be hesitant in saying categorically that size is not a relevant factor. By examining the individual slopes in the graphs, it is evident that certain combinations of age and size have a marked effect on mating ability and one must realize that when a given factor is examined, the other factor is averaged out.

The knowledge obtained as a result of this investigation represents just a beginning in the understanding of the mating of king crabs. To what extent these findings are applicable to mating in nature remain uncertain. The effects of holding experimental crabs in undersea pens must be understood before realizing full application of the data to practical management of the fishery.

Holding males in pens could adversely affect mating ability of some classes, particularly later matings after prolonged captivity, while simultaneously enhancing ability of others by forcing partners into constant close association with one another. Larger females used later in the experiment may also have affected results.

Even though size does not appear to be a significant factor in mating ability as far as the number of repeated matings is concerned, and even though small males appear to be capable breeders, it remains a possibility that in some instances in nature small males may not serve adequately as brood stock. Measurements of 6,804 king crabs captured by divers as mating pairs, 1963-1971, reveal that small young females are the first to mate each season followed three months later by large old females (Powell, Rothschild, and Buss, 1972). Further, males mating in nature with "pubescent" females (i.e., those mating for the first time and therefore the smallest found) are older and larger, averaging 42 mm more than females, with grasping observed as early as January 9 (Powell, Shafford, and Jones, 1972).

Apparently male size and male-female ratios are not the only factors affecting mating in nature. The presence in recent years of high incidence of adult females without eggs and with partial clutches within certain locations of the Kodiak fishery seem to be fishery-related because they occur only in areas of intense fishing (Powell, 1969[7]).

Adult female king crabs form mating congregations in shallow water from January through April and these congregations are intermittently distributed throughout the thousands of square miles of shallow habitat. For mating to be successful in each congregation, adequate numbers of capable males must be present during the relatively brief matable period following female ecdysis, otherwise delayed mating may adversely affect the success of ovulation and subsequent fertilization (Kurata, 1961; McMullen, 1969; and Wallace, Pertuit, and Hvatum, 1958).

The ratio of males to females necessary for complete mating success in nature appears dependent upon factors other than just numbers alone. The rate at which females molt and spatial distribution and size differences of adults inhabiting the location are also believed important. The greater the rate of female molting, the greater the number of males required. Male crabs select partners as early as 16 days prior to mating and continually grasp them until copulation occurs soon after female ecdysis (Powell, Rothschild, and Buss, 1972). Because of premating "grasping" behavior, it is possible that females molt without male partners though a

[7] Powell, Guy C. 1969. Some aspects of king crab biology. Proc. Am. Fish. Soc., West. Div. Meeting, Jackson Hole, WY, June 1969. (Processed)

favorable male-female ratio exists, because all males are either preoccupied grasping other females or resting between subsequent matings.

King crabs segregate to varying degrees according to size, sex, age, and time of year. Commercial fishing is concentrated in areas inhabited by large males with total effort varying according to factors such as accessibility. Thus cropping of males may be excessive in one area but not in another. Incidence of nonovigerous adult females is lowest in areas where sublegal sized males are abundant, but is often high in exploited areas with few adult males (unpublished, Alaska Dept. Fish & Game).

Size differences between partners, presence of competing males, and time of year also must be considered in evaluating the reproductive potential of mating populations.

It is conceivable that even with many young adult males present, a population of large old females may be inadequately serviced partly because the few surviving large males may, through aggressive behavior, keep smaller males away. To what extent competitive behavior exists is presently unknown but large old males commonly are found mating small young females in nature. Of the 14 matings in this experiment, where females were larger than males, 79 percent produced partial clutches.

Small males probably produce less reproductive material (sperm) than large males, and as a result, may be less capable of fertilizing the greater masses of eggs of large females.

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AN EVALUATION OF MID-WATER ARTIFICIAL STRUCTURES FOR ATTRACTING COASTAL PELAGIC FISHES[1]

DONALD A. WICKHAM AND GARY M. RUSSELL[2]

ABSTRACT

Mid-water artificial structures positioned off Panama City, Fla. during August 1970 were evaluated to determine their ability to attract coastal pelagic fishes. Quantitative and qualitative experimental results were obtained using scuba divers and purse seine catches. The feasibility of using artificial structures to facilitate the commercial harvest of coastal pelagic fishes with purse seines was established and the methods described. Average catch values of 398 kg (875 lb) per structure were obtained during a period when coastal pelagic fishes were unavailable to the local fishery. A greater total production was obtained from structures fished daily compared with those allowed to soak for 3 days before being fished. Experimental purse seine collections established that fish leave the structures at night with new recruitment occurring daily. No significant differences were obtained from preliminary experiments to evaluate the effects of structure size and color on attraction effectiveness. A working hypothesis is presented to describe apparent behavioral mechanisms involved in the attraction of some species of coastal pelagic schooling fish to objects in the sea. This study indicates that artificial-structure fish-attraction has potential for development as a technique to facilitate the harvest of the latent coastal pelagic fishery resources in the Gulf of Mexico.

Artificial structures have been shown to be effective for attracting concentrations of pelagic fishes (Hunter and Mitchell, 1968). Klima and Wickham (1971) visually evaluated the species and number of coastal pelagic fishes attracted to experimental artificial structures in the northeastern Gulf of Mexico. These observations established the feasibility of attracting large numbers of coastal pelagic fishes with artificial structures; however, many questions concerning structure attraction characteristics and dynamics as well as their actual usefulness in augmenting conventional harvesting methods for these species still remained unanswered.

Studies were conducted during August 1970, in 5 to 10 fathoms (9 to 18 m) of water offshore of Shell Island, Panama City, Fla. to obtain quantitative samples for evaluating the validity of scuba-diver estimates of structure-attracted fish aggregations, to evaluate methods for using a conventional purse seine for capturing structure-attracted fish, and to obtain catch-production values for single structures. We also evaluated effects of structure soak time and size-color differences on attraction effectiveness. Day and night samples, plus scuba-diver observations of fish behavior, provided additional clues to the dynamics of the coastal pelagic fish aggregations attracted to artificial structures.

MATERIALS AND METHODS

Our fish attraction devices were three-dimensional structures. Each structure was constructed from vinyl-cloth covered, wood and wire frame panels. Two panels were fastened along one side, permitting the structure to be stored flat, but opened into a three-dimensional right prism when deployed for fish attraction. Two sizes of structures were used. The small structure panels were 0.9×1.5 m (3×5 ft) in size and the large structures, with twice the surface area of the smaller structures, were 1.8×1.5 m (6×5 ft). All structures were white except those painted for specific experiments.

Structures were positioned 4-6 m (15-20 ft) beneath the surface. The structure design and mooring arrangement are illustrated in Figure 1. Structures were spaced at approximately 0.8-km

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FISHERY BULLETIN: VOL. 72, NO. 1, 1974.

(0.5-mile) intervals. Their arrangement in the experimental site is shown in Figure 2. The eight structure mooring locations were used with different structures as required for specific experiments.

The 15-m (49-ft) single boat-rig bait purse seiner, *Gulf Ranger*, was chartered to make quantitative collections at selected artificial structures using a tom-weight type purse seine, 22 m (12 fathoms) deep and 110 m (60 fathoms) in length, with 3.2 cm (1¼-inch) stretched mesh webbing. A 6-m (20-ft) inboard-outdrive power boat was used as a diving platform and for picking up and resetting structures sampled by the purse seine.

Daily visual estimates of the number and species of fish present at each structure were made independently by scuba divers. We obtained quantitative data from selected structures by collecting all the fish around these structures with the purse seine. Diver estimates and purse seine catch data are given in Table 1.

Scuba divers made visual estimates of the fish aggregation at a structure prior to beginning the purse seine set. The structure anchor was picked

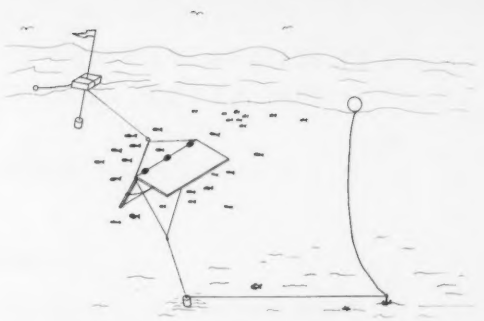

FIGURE 1.—Artificial structure design and mooring arrangement.

up by the divers as soon as the seiner began setting its net. When pursing was half completed, the structure counterweight was retrieved to prevent its being tangled in the purse line. After the purse rings were up, the dive boat would take the structure aboard, pass over the cork-line, and reset the structure clear of the net.

The captain of the *Gulf Ranger* estimated the catch weight after each purse seine set and the biologist aboard sampled each catch to provide

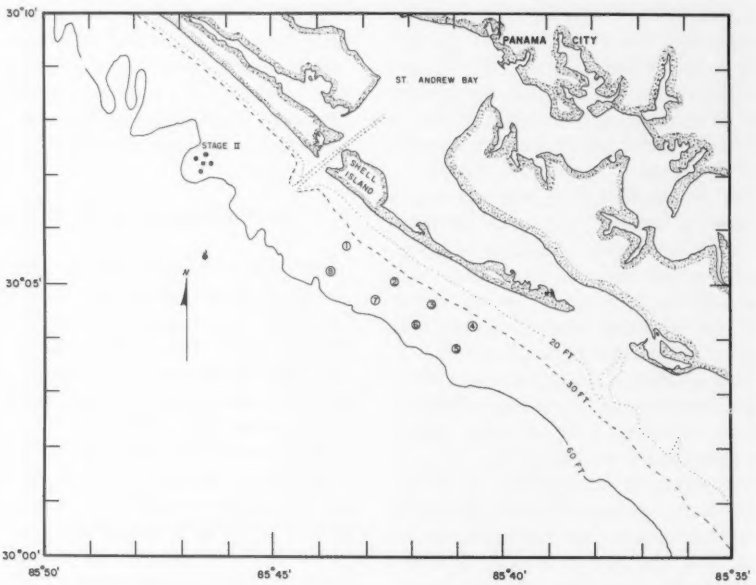

FIGURE 2.—Map of experimental site with numbered circles illustrating positions where artificial structures were deployed. Stage II is a Navy research platform west of the study area.

TABLE 1.—Diver estimates and purse seine catches.

Structure position		1		2		3		4		5		6		7		8	
Structure type		Large white		Small white		Large white		Small white		Large white		Small white		Large white		Small white	
Date 1970	Sample type	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)
July																	
12	Diver 1	1330	227	1415	22	1531	681	1557	227	1635	136	1702	136	1726	454	Lost-No observations	
	Diver 2		272		68		681		136		318		227		454		
	Average		250		45		681		181		227		181		454	—	—
13	Diver 1	1010	136	1034	454	1110	136	1133	136	1200	454	1235	136	1300	454	—	—
	Diver 2		227		227		136		136		272		90		227		—
	Average		181		340		136		136		363		113		340		—
14	Diver 2	1037	136	1100	227	1125	227	1215	227	1150	227	1241	136	1309	227	—	—
	Diver 3		227		136		136		227		90		363		227		—
	Average		181		181		181		227		159		250		227		—
15	Diver 2	1045	227	1130	454	1215	681	1240	454	1305	681	1345	454	Lost-No observations			
	Diver 3		227		454		909		454		909		454		—	—	—
	Average		227		454		795		454		795		454		—		—
16	Diver 1	0945	681	1015	318	1045	454	1110	454	1137	681	1207	90	—	—	—	—
	Diver 3		454		454		909		318		909		90		—		—
	Average		568		386		681		386		795		90		—		—
17	Diver 1	1202	227	1227	227	1255	136	1316	90	1356	136	1418	136	—	—	—	—
	Diver 2		227		454		227		136		136		136		—		—
	Average		227		340		181		113		136		136		—		—
18	Diver 1	0947	136	1013	227	1045	318	1105	136	1130	45	1200	136	—	—	—	—
	Diver 2		227		227		227		136		45		454		—		—
	Average		181		227		272		136		45		295		—		—
20	Diver 2	0945	136	1300	45	1010	136	1245	227	1150	136	1135	136	1315	909	1045	136
	Diver 3		90		681		136		181		90		227		909		136
	Average		113		363		136		204		113		181		909		136
	Purse seine	0945	90	1600	90	—	—	—	—	—	—	—	—	1403	1,363	1105	45
August																	
17	Diver 1	0953	454	1533	45	1031	68	1100	454	1325	1,136	1346	90	1406	454	1121	454
	Diver 3		227		136		136		454		909		90		227		454
	Average		340		90		102		454		1,022		90		340		454
	Purse seine	1100	363	1730	363	—	—	—	—	—	—	—	—	1630	681	1400	818
18	Diver 2	0940	45	1320	454	1255	454	1020	909	1130	454	1200	454	1220	363	1050	227
	Diver 3		22		454		454		2,272		454		2,272		454		90
	Average		34		454		454		1,590		454		1,363		409		159
	Purse seine	1000	90	1350	318	—	—	—	—	—	—	—	—	1230	454	1105	227
19	Diver 2	0915	90	1250	45	1415	454	1650	909	1600	227	1505	272	1140	363	1050	227
	Diver 3		136		227		454		909		227		227		227		136
	Average		113		136		454		909		227		250		295		181
	Purse seine	0830	68	1400	454	1500	454	1715	909	1620	454	1540	272	1245	681	1130	545
20	Diver 1	1225	136	1515	454	1715	454	1700	681	1630	681	1610	681	1430	363	1335	136
	Diver 2		227		454		454		454		1,136		909		454		227
	Average		181		454		454		568		909		795		409		181
	Purse seine	1300	409	1550	363	2145	45	2040	45	2305	9	2230	45	1445	454	1350	272
21	Diver 2	1240	36	1425	227	—	No observation	1700	454	1635	1,363	1620	454	1555	363	1340	227
	Diver 3		22		318		—		681		1,136		681		363		90
	Average		34		272		—		568		1,250		568		363		159
	Purse seine	1300	90	1500	45	—	—	2030	45	2115	9	2220	11	1600	454	1355	363
22	Diver 1	1243	136	1347	227	1406	454	1425	227	1505	681	1443	454	1326	227	1306	363
	Diver 3		136		454		363		227		1,363		909		363		318
	Average		136		340		409		227		1,022		681		295		340

TABLE 1.—Diver estimates and purse seine catches.—Continued.

Structure position		1-4		1-4		1-4		1-4		5		6		7	
Structure type		Small white		Small blue		Small green		Small yellow		Large white		Large white		Large white	
Date 1970	Sample type	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)
August															
24	Diver 2	1300	136	1335	227	1430	272	1535	454	—	—	—	—	—	—
	Diver 3		136		363		227		454		—		—		—
	Average		136		295		250		454		—		—		—
	Purse seine	1305	113	1400	454	1505	272	1615	318	—	—	—	—	—	—
25	Diver 2	1500	454	1245	227	1625	454	1430	136	1725	818	1705	681	1600	909
	Diver 3		454		22		363		227		909		909		909
	Average		454		125		409		181		863		795		909
	Purse seine	1530	363	1245	113	1630	363	1430	272	1730	272	2200	13	2245	[1]454
26	Diver 1	1212	909	1455	909	1132	318	1330	136	1600	681	1437	1,363	1538	227
	Diver 3		909		909		454		227		909		1,363		909
	Average		909		909		386		181		795		1,363		568
	Purse seine	1255	409	1515	68	1145	113	1405	113	1610	363	—	—	—	—
27	Diver 1	1440	454	1345	227	1245	454	1140	454	1540	454	1420	454	1530	1,363
	Diver 2		1,363		454		454		909		909		454		909
	Average		909		340		454		681		681		454		1,136
	Purse seine	1500	90	1400	272	1300	113	1200	227	1600	181	1700	[2]1,363	—	—

[1] Set around nightlight.
[2] 1,136 kilograms little tunny.

data on species composition. It was not practical to totally weigh each catch as it came aboard or to keep the fish from individual sets separated for later weighing; consequently the captain's catch weight estimates had to serve as our quantitative standard. The accuracy of the captain's estimates was established by comparing the daily total of his estimates with the daily fish house landing records for the *Gulf Ranger* (Table 2). We believed the accuracy of these estimates ($r^2 = 0.97$) justified our utilizing them for evaluating diver estimates and for quantifying experimental data (Figure 3).

RESULTS

Diver Estimates

The validity of scuba-diver observations was evaluated by comparing the divers' estimates of the total number and species composition of fish present at a structure with data obtained from the purse seine catch at that structure. Numerical estimates obtained by the divers for coastal pelagic school fish were converted to weight, utilizing a catch average of approximately 22 fish per kilogram to permit comparison with purse seine catch data.

The comparison of diver estimates with the captain's estimates for the corresponding purse seine catches are plotted in Figure 4 for data collected 17-21 August 1970 (Table 1). Data from 24 August to 27 August were not included in this comparison because schools of little tunny (*Euthynnus alletteratus*) began following the purse seiner and were occasionally observed attacking and scattering the structure-attracted fish schools before the purse seine set was completed. A linear regression analysis of the mean for each set of paired diver estimates ($Y = 76.5 + 0.56X$; $r^2 = 0.68$) indicates that although considerable variation does exist, fish schools less than 182 kg (400 lb) tend to be slightly overestimated while the larger schools are increasingly underestimated. A linear regression analysis was also calculated for each diver's individual estimates and these calculations indicated that estimates made by diver 2 tend to be more accurate than the more conservative estimates made by divers 1 and 3.

The purse seine catch sample data indicated scuba divers were able to identify the major

TABLE 2.—Diver estimates, purse seiner captain's estimates, and fish house landing totals for daily catches from artificial structures.

Date 1970	No. daytime sets	Total average diver estimates for structures sampled	Total purse seiner captain's daily catch estimates	Fish house landings	Fish house landings by species	
					Round scad	Spanish sardine
		kilograms				
August						
17	4	1,227	2,227	2,193	830	1,363
18	4	1,057	1,091	909	614	295
19	8	2,568	3,841	4,045	1,830	2,215
20	4	1,227	1,500	1,545	727	818
21	4	830	955	852	432	420
Total	24	6,909	9,614	9,544	4,433	5,111
[1]21	4	1,136	1,159	1,034	761	273
[1]25	5	2,034	1,386	1,682	716	966
[1]26	5	3,182	1,068	693	443	250
[1]27	6	3,523	1,114	1,194	489	705
Total	20	9,875	4,727	4,603	2,409	2,194
9-day total	44	16,784	14,341	14,147	6,842	7,305

[1] Data not used for scuba-diver estimates-purse seiner catch comparisons.

species attracted to the structures. They were not, however, able to determine accurately the percent species composition for the schools of mixed coastal pelagic fishes. These mixed schools contributed over 95% of the catch weight taken from each structure. The mixed coastal pelagic school fish consisted of round scad *(Decapterus punctatus)* and Spanish sardine *(Sardinella anchovia)*. The bait fish occurred at each structure in mixed schools of varying percent species composition. The difficulty encountered by the divers in obtaining accurate percent species composition data for this group was probably the result of behavioral differences between the species. Round scad usually approached closer to the divers than Spanish sardine, which tended to concentrate on the side of the school farthest away from the divers.

Jacks usually represented less than 5% of the total catch weight and consisted primarily of small 15-cm (6-inch) blue runner (*Caranx crysos*), crevalle jack (*C. hippos*), and bar jack (*C. ruber*). Among the species which comprised the major components of Klima and Wickham's (1971) jack group, amberjack (*Seriola* sp.) were only occasionally observed and rainbow runner (*Elagatis bipinnulata*) were notable by their absence in this series of experiments. The jacks are not treated separately in our paper because of their minor contribution to the total number and weight of the structure-attracted fish aggregations.

Comparison of diver estimates and purse seine catch data indicates that although purse seine data are quantitatively superior both sampling techniques are complementary and, combined, provide a more complete picture of the experimental environment than either singularly. Where diver estimates provided the only available data they are considered sufficient to permit rough evaluation of the experimental results in terms of their commercial significance.

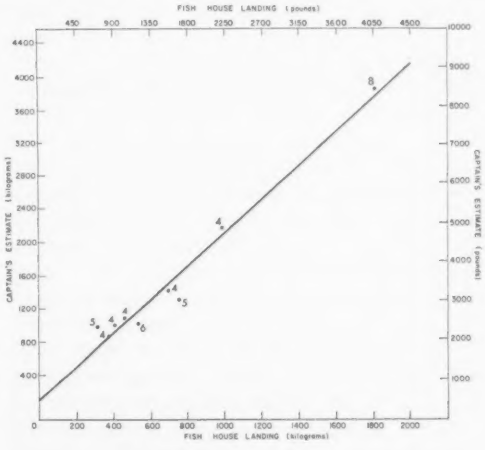

FIGURE 3.—Relationship between the daily total of the *Gulf Ranger* captain's estimates of structure-purse seine catches and the daily fish house landing records. Statistical evaluation of this data by linear regression analysis yields $Y = 216.4 + 0.876X$; $r^2 = 0.97$. N = number of set estimates in each daily total.

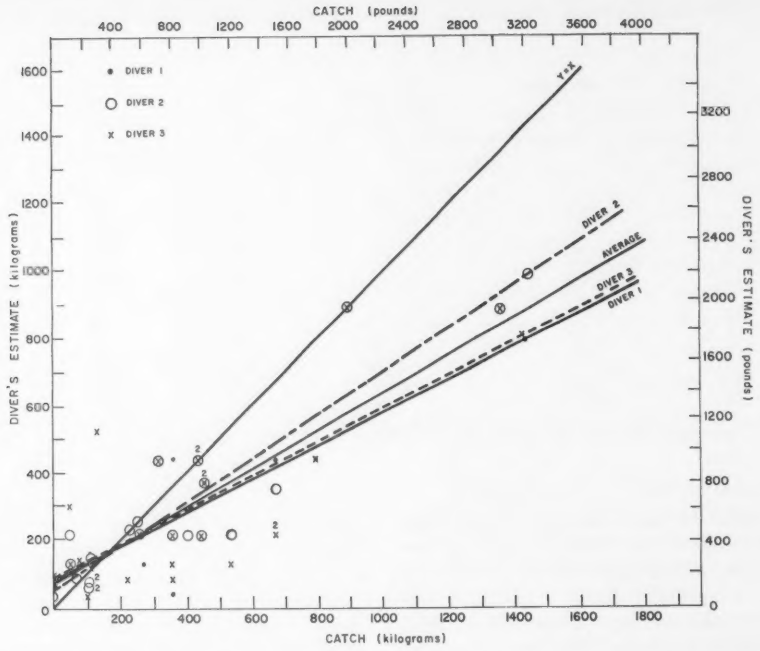

FIGURE 4.—Relationship between divers' estimates of bait fish school size and the captain's estimate of the purse seine catch at each structure. A linear regression analysis of the average paired diver estimates yields $Y = 76.5 + 0.56X$; $R^2 = 0.684$. A linear regression analysis of the estimates made by each diver yields $Y = 77.6 + 0.504X$; $r^2 = 0.285$ for diver one; $Y = 55.3 + 0.683X$; $r^2 = 0.704$ for diver two; and $Y = 98.4 + 0.501X$; $r^2 = 0.42$ for diver three.

Recruitment Patterns and Production

Our observations indicate a rapid recruitment with fish being observed at structures the day following placement. To obtain estimates of production and recruitment of bait fish to the structures, we made daily diver estimates and purse seine collections at four selected structures. Four other structures, also observed daily by divers, were set on after being in position for 3 days. During this period (17-21 August 1970), our structures produced an average of 398 kg (875 lb) per set. These catch rates are not extremely large, but they were made when bait fish were not seasonally available to the local beach seine fishery. No bait was being landed, except for fish captured around our structures. The total daily diver estimates and purse seine collections are plotted in Figure 5, along with the 3-day accumulative totals, to allow comparison of production between the four structures fished daily and the four structures set on once, following the 3-day soak period. Our day 3 catch results indicate no significant advantage in catch size was realized by allowing the structures to soak for 3 days. The potential total catch, assuming daily sets had been made on the 3-day soak structures, indicated from our consistently conservative diver estimates was three times larger than the actual catch after 3 days' soaking. The total accumulative catch from the four structures set on daily was also approximately three times larger than the actual catch from the four 3-day soak structures even though diver estimates indicated smaller total fish concentrations were present at the structures set on daily. These results show that a greater total production was obtained by making daily sets. This high rate of daily attraction and the apparent lack of fish accumulation provided further indications

that fish were being attracted to the structures on a daily basis.

Comparison of Day and Night Collections

A series of day and night sets were conducted to determine whether fish leave the structures at night. Divers estimated the quantities of fish at four selected structures which were then set on during daylight hours. The quantity of fish at four other structures was estimated by divers just before dark and fish around these structures were collected after dark. Diver estimates, and day and night catch results, are plotted in Figure 6. The diver estimates were conservative for structures set on during the day, with estimates for both days being less than the actual catch for three of the four structures. The divers frequently estimated that concentrations of fish present at the structures fished at night were larger than at the structures fished in the daylight. Nighttime collections however, consistently produced only 45.5 kg (100 lb) or less of mixed species. These results provided further evidence that bait fish leave the structures at night and that new recruitment was occurring daily. The nighttime sets were made during the new moon and we lack data on whether bait fish also leave the structures at night during the full moon.

Size and Color Evaluation

The success of bait fish attraction with artificial structures appeared to be dependent upon the visibility of the structure. We evaluated two sizes of structures to determine whether doubling the structure size would increase the number of fish attracted. An analysis of variance for purse seine capture data ($F = 0.75 < F_{0.90(1,5)} = 4.06$) and diver estimates revealed no significant difference in attraction by structure size.

Structure attraction was also evaluated in terms of color visibility. We compared a white structure with ones painted fluorescent green, blue, and yellow since Kinney (1970) reported that fluorescent paints provide greater visibility under water. Structure position was rotated daily so that a structure of each color occupied each of the four positions. An analysis of variance for catch data ($F = 0.026 < F_{0.90(3,9)} = 2.8$) and diver estimates revealed no significant

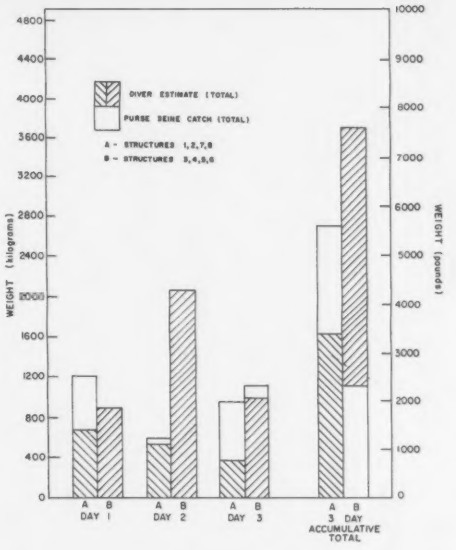

FIGURE 5.—Total of daily average diver estimates and purse seine catch weights, 17-19 August 1970. (A) Structures estimated by divers and fished daily by purse seine. (B) Structures estimated daily by divers but fished by purse seine only on day three.

difference in the number of fish attracted to the structures on the basis of color. During these color evaluation studies, the bait fish schools were occasionally scattered by little tunny. These predator attacks may have affected the catch data; however our diver estimates were not affected and also indicate no significant color preference.

Divers reported the experimental changes in size and color extended the visible range of a single structure less than 2.1 m (6 ft) which apparently was not sufficient to significantly improve the structures' attraction capabilities.

Structure placement (Figure 3) in relation to the distance offshore (water depth) or to the along-shore current direction tended to have some effect on the number of fish attracted, with larger numbers of fish being attracted to structures positioned offshore than to those positioned inshore. Structures positioned on the eastern end of the experimental area also tended to attract more fish than those on the western end. These general patterns probably vary with seasonal changes in water temperature and prevailing current direction. Our experiment was

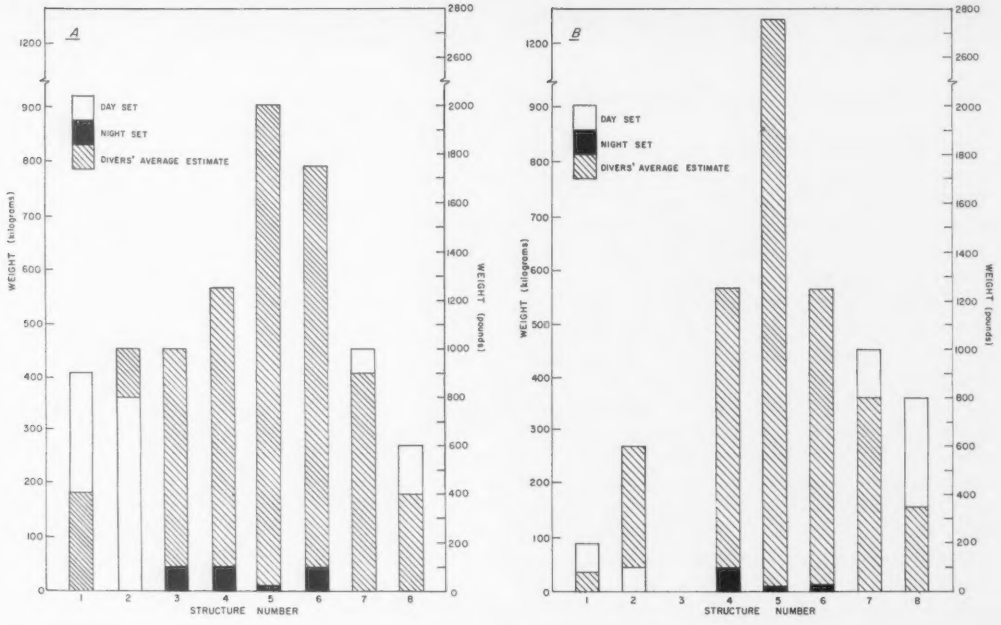

FIGURE 6.—Average diver estimates and day and night purse seine catch weights for each structure on (A) August 20, and (B) August 21, 1970. No diver observations or purse seine sets were made at structure three on August 21 due to an afternoon squall.

not designed to evaluate the effects of structure placement on fish attraction and further studies would be necessary to meaningfully evaluate these effects.

Responses to Moving Structures

A bait fish school was observed by Klima and Wickham (1971) to have remained with a free drifting artificial structure moving slower than the current. One of our structures (Structure No. 8, 19 August 1970), with a school of bait fish in attendance, was also observed dragging its anchor and moving slowly with the current. This structure was towed for 20 min at a speed of approximately 2 knots against a 0.5 knot current for a distance of approximately 0.8 km (0.5 mile) in order to return it to its experimental mooring location. The structure moved up to the surface while being towed, but the fish swam along with it, trailing out behind when the towing speed was increased. After the structure was reanchored in position, the fish school began swimming around it in the usual manner. Divers estimated that over half the original number of fish remained around the structure after towing. A purse seine set made on this structure after repositioning produced 545 kg (1,200 lb) of fish.

Behavior Observations at Structures

Our observation of bait-fish-school behavior at the structures is in general accordance with the behavior described by Klima and Wickham (1971). The bait-fish schools normally maintained a position up-current from the structures and were observed continuously feeding on crab larvae and other particulate material in the water. During very slow or zero current conditions, the bait fish would often mill about in a loose aggregation (Figure 7) or form long streaming schools making large looping passes out and around the structures in all directions. The schools would frequently swim beyond the divers' range of visibility, remaining out of sight for periods up to 3 min or longer before streaming back in and around the structures from a different direction.

FIGURE 7.—Underwater photograph of a mixed school of round scad *(Decapterus punctatus)* and Spanish sardine *(Sardinella anchovia)* swimming past an artificial structure.

A different pattern of behavior was observed by the divers when the bait-fish schools were threatened by the presence of feeding predators, i.e., Spanish mackerel (*Scomberomorus maculatus*), king mackerel (*S. cavalla*), little tunny (*E. alletteratus*), and bluefish (*Pomatomus saltatrix*). On these occasions, relatively small bait-fish schools, i.e., 100 kg (220 lb) or less, would form a milling ring with the structure in the center or swirl in a tight group in quick passes close to the structure as the predators made darting attacks on the school. Larger schools would usually be split by the attacking predators with one group of bait fish moving to the structure and circling it as described above while the remaining fish moved off in tight, fast-darting groups.

Behavioral Mechanisms

Different sizes and species of fish apparently associate with objects in the sea for different reasons involving different behavioral mechanisms. Hypotheses advanced to explain the association of fishes with floating objects were reviewed by Gooding and Magnuson (1967). The initial attraction of pelagic fishes to objects probably results from their visually detecting the object in the optical void of the pelagic environment, since fish beyond the visual range of a structure or structure-attracted fish school are not attracted (Hunter and Mitchell, 1967). Significantly improving the visual characteristics of an object apparently increases the rate and number of fish it attracts (Hunter and Mitchell, 1967; Klima and Wickham, 1971). Objects, however, must serve a meaningful function beyond that involved in the initial visual attraction in order for pelagic fish to remain in association with them. To tentatively explain this behavior in mixed schools of round scad *(D. punctatus)* and Spanish sardine *(S. anchovia)* around artificial structures, Klima and Wickham (1971) proposed the hypothesis: "Floating objects and underwater structures provide spatial references around which fish can orient in the otherwise unstructured pelagic environment." This tentative hypothesis was given some support by our study, but it must be modified and expanded to account for our additional behavioral observations. Our studies indicate that although coastal

pelagic bait fish are capable of ranging beyond sight of an object for periods of several minutes or longer, they apparently require periodic visual reconfirmation of the object's position in order to maintain their orientation with it. This assumption is supported by our observations that structure-attracted fish aggregations leave the structures at night when low light levels inhibit visual contact. Our observations of coastal pelagic bait-fish behavior around artificial structures also indicate that the structures can apparently be useful to these species for predator avoidance. Schools of bait fish associated with an artificial structure have been observed to be immediately attacked by predators upon removal of the structure from the water. Bait-fish schools threatened by the presence of feeding predators were observed to form a tight ball or ring around the structure or swirl in tightly packed formation making quick darting passes near the structure. On several occasions, we have observed the attack behavior of a predator to be interrupted at the moment the bait fish darted past the structure. Mitchell and Hunter (1970) describe laboratory experiments in which splitnose rockfish *(Sebastes diploproa)* and opaleye *(Girella nigricans)* were pursued more often, for longer periods, and captured more frequently by ocean whitefish *(Caulolatilus princeps)* in an aquarium when kelp was absent than when it was present.

Our present supposition as to the possible mechanisms involved in the association of some species of coastal pelagic schooling fish with objects in the sea are summarized in the following working hypothesis: "Objects in the sea provide visual stimuli which attract certain species of pelagic schooling fish and are used in conjunction with natural optomotor responses to provide a spatial reference for orientation in the otherwise relatively unstructured pelagic environment; however, in the presence of feeding predators stimulus priorities are restructured such that the objects become useful for predator avoidance." An increasing body of subjective evidence is available to support much of this conjecture, but its verification lacks the requisite quantitative experimental evidence.

Purse Seine Operations

The feasibility of harvesting structure-attracted coastal pelagic bait fish with conventional tom-weight type purse seines was evaluated during our development of the quantitative collection procedures. Fish aggregations normally showed little disturbance during purse seine sets while the structure remained in the water. Fish stayed with the structure even when it floated at the surface after the counterweight was lifted to prevent its tangling the purse line. The fish showed distress and attempted to escape the net only when the structure was removed from the water and the diving boat prepared to pass over the corkline and reset the structure. The only deviation from this pattern was observed when bait fish were attacked by predators, i.e., little tunny *(E. alletteratus)*, which on several occasions were following the seiner. On these occasions, the predators scattered the bait fish during the set and then escaped before the net was completely closed.

During our experimental collections, we utilized an additional small boat and several men to handle the structures during the purse seine operations. Sets have been made, however, using only the seine skiff and its operator to retrieve and reset the structures. These trials indicate that in a commercial fishing operation using artificial structures, fishing procedures can be modified so that additional men and equipment should not be required. The applicability of structure-attraction techniques for augmenting purse seining during commercial fishing operations, although technically feasible, remains dependent upon the production potential of structures and their recruitment characteristics in the geographical area under consideration.

SUMMARY AND CONCLUSIONS

An evaluation of our diver estimates and purse seine catch data indicates that a combination of these techniques provides a more complete description of the artificial structure experimental environment than either singularly. Our comparative results support the contention by Klima and Wickham (1971) that quantitative diver estimates tend to be conservative where large fish schools are involved. Our divers were able to qualitatively determine the major species present at a structure, but were unable to reliably establish the percent species composition in mixed species schools.

The quantity of fish attracted to the structures during our study was not as large as the schools reported by Klima and Wickham (1971). Coastal pelagic school fish, however, were seasonally unavailable to the local fishery during the study period and the fish captured around our structures were the only bait fish being landed.

The rapid rate of recruitment during our study was similar to the pattern of recruitment reported by Klima and Wickham (1971) with fish being observed at the structures the day following placement. Our experimental results indicated that the fish were recruited to the structures daily and no significant accumulation in the fish population was observed when the structures were allowed to soak for 3 days. Consequently, a greater total production was obtained from the structures by making daily sets. Comparative day and night sets provided further evidence that fish schools dispersed from structures at night during the new moon and new fish were being recruited each day.

We were unable to significantly improve the rate or number of fish attracted to a structure either by doubling its size in relation to our standard structure, or by painting it with fluorescent colors. The experimental changes in size and color apparently did not extend the visible range of a structure sufficiently to significantly increase the number of fish attracted. Further study is required to determine whether multiple structure units might be successful as a means for significantly improving the effective range of structure attraction.

The feasibility of harvesting structure-attracted coastal pelagic bait-fish schools with conventional tom-weight purse seines was established by the success of our quantitative collection procedures. The incidence of successful purse seine sets was greatly improved using the artificial structure techniques since the coastal pelagic fish schools remained in association with the structures during the sets and made no attempt to escape.

Our experience during this study indicates that artificial-structure fish attraction techniques can be developed to facilitate the harvest of the latent coastal pelagic resources in the Gulf of Mexico. Artificial-structure fish attraction techniques may also have sport fishing applications, potential for development as a method for providing ground truth for fishery survey remote sensor evaluation and as a method for monitoring fish movements and relative changes in abundance in certain geographical areas. These potential applications for artificial-structure fish attraction techniques will be the subject of future investigations.

ACKNOWLEDGMENTS

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THE AGE COMPOSITION OF STRIPED BASS CATCHES IN VIRGINIA RIVERS, 1967-1971, AND A DESCRIPTION OF THE FISHERY[1]

GEORGE C. GRANT[2]

ABSTRACT

The age composition of Virginia catches of the striped bass, *Morone saxatilis*, is being monitored as one of the parameters important in rational management of the species. Catches of pound nets and fyke nets, relatively nonselective gear types used in estimates of age structure, were sampled semimonthly in three Virginia rivers from July 1967 through June 1971.

Seasonal changes in age composition are slight with older, migratory striped bass occurring more frequently in winter and spring catches. Young fish are not caught by these nets in significant numbers until the spring following the year of their hatch. An age group that is dominant in summer usually continues its dominance through the spring of the following year.

Differences in age composition of striped bass catches among rivers and years occur as a result of variable year class strength. Although one-year-olds normally dominate catches, two-year-olds may predominate either through local failure of a year class or by continued dominance of a relatively strong year class.

A brief description of the striped bass fishery in Virginia is included.

Closer management of anadromous fish stocks may become necessary as a protective response to increasing human populations along the Atlantic coast of the United States. Because of their reproductive migrations into river systems, these anadromous fishes may be most directly affected by the expanding megalopolis of the east coast and the increased pollution of coastal waters.

One valuable anadromous species is the striped bass, *Morone saxatilis* (Walbaum). Although the biology and habits of striped bass are fairly well studied (Raney, 1952), effective management of the stocks has been hampered by the absence of data on population parameters such as age composition and mortality.

An investigation of striped bass in Virginia[3] was initiated in 1967 after a review of results from the Chesapeake Bay Cooperative Striped Bass Program (Lewis, 1961; Mansueti, 1961; Massmann and Pacheco, 1961) and follows the suggestions of Sykes (1961) for further research on striped bass. This paper considers the age composition of striped bass catches in Virginia and briefly describes the fishery.

DESCRIPTION OF THE FISHERY

The coastal Virginia fishery for striped bass is scattered and diverse. It includes trawlers, pound nets, fyke nets, haul seines, gill nets and sport fishing gear.

In the commercial fishery, pound nets are fished at permanent locations and are most consistently in use. They are lifted only during brief periods for cleaning, to prevent possible ice damage, or because of nuisance factors such as abundant jellyfish. Fyke nets, hung and fished much like small pound nets in Virginia waters, are usually located farther upriver than the pound nets. Catches are relatively small and the gear is employed more sporadically than pound nets. Trawlers are limited to offshore fishing by law. Therefore striped bass are available to this gear only in winter months, when they are migrating along the coast. Striped bass availability to trawlers increases during severe winters when the river populations migrate to the warmer coastal waters (Grant et al., 1970). Gill net mesh size and manner of fishing vary with the season in the striped bass fishery. Small mesh "spot and perch nets"

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(2⅞ - 3½" stretch mesh) are anchored in the summer and staked from late fall to winter. Large mesh "shad nets" (5½" stretch mesh) are staked or drifted in late winter and spring. Haul seines are used sporadically throughout the warmer months, but most effectively in the spring.

Sport fishing for striped bass is intensive in the lower Chesapeake Bay, especially along the Chesapeake Bay Bridge-Tunnel in spring and fall. The sport fishery extends from the mouth of the Bay to the freshwater regions of major river systems from March through December. Attraction of small striped bass to the numerous lighted piers extends sport fishing well beyond daylight hours.

Commercial landings of striped bass in Virginia[4] for the 40-yr period 1930-1969 show a ninefold increase from a low of 0.3 million pounds in 1934 to 2.8 million pounds in 1966 (Figure 1). The overall trend in landings (and striped bass populations) has been rising during this period. Two definite peaks of abundance are evident, one in the late 1940's and the other in the 1960's. Not included in these landings are sport catches, which have increased to as much as 50 percent of the total catch in certain areas (Grant, unpublished data). Averaged commercial landings in the most recent years have declined; continuation or reversal of this decline depends on contributions to subsequent catches by successful year classes such as those of 1966 and 1970 (Grant and Joseph, 1969; Grant, Burrell, and Kriete, 1971).

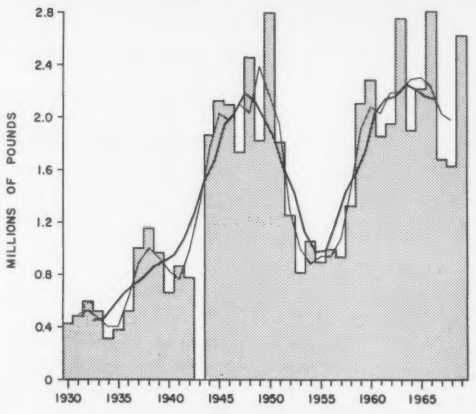

FIGURE 1.—Annual landings of striped bass in Virginia, 1930-69. Moving averages (indicated by heavy line for 6-yr average and light line for 3-yr average) incorporate an interpolated value of 1,321,000 pounds for 1943.

AGE COMPOSITION

Methods and Materials

Pound nets and fyke nets trap striped bass over their entire size range, except for the young-of-the-year which are incompletely recruited to the gear. These two gear types were, therefore, considered to be essentially nonselective (allowing for escapement of Age 0 fish) and were sampled for estimates of the age composition of striped bass stocks residing in the James, York, and Rappahannock rivers. Although differences in the age composition of catches by pound and fyke nets did occur, no consistency was evident in these differences, so catches were pooled for analysis. Rappahannock River samples were taken from pound nets only.

The scale method was used for age determinations. Scales were first used in age analysis of striped bass populations by Scofield (1931); this method was fully developed and validated for striped bass by Merriman (1941). Samples of approximately 50 striped bass were obtained from each river system semimonthly. Scales were removed from individual fish at the site specified by Merriman (1941). Cellulose acetate impressions of scale sculpturing were prepared using five or six scales from each fish. Annuli were counted at a magnification of 15× with all scales being read at least twice and instances of disagreement re-examined.

Annuli on the scales of Virginia striped bass form between April and June, coincident with the spawning season and hatch of a new year class. The growth year of local populations, therefore, may be considered to extend from July to June. Young-of-the-year do not become Age I fish until late spring of the year following their hatch. In this paper, July 1 is designated as the start of each year so that a member of the 1966 year class caught between 1 July 1967 and 30 June 1968 would be called Age I. Seasonal designations are used as follows: winter (Jan.-Mar.), spring (Apr.-June), summer (July-Sept.), fall (Oct.-Dec.); these quarterly periods

[4] Data from Koo (1970) and from annual summaries of regional fisheries statistics published by the Bureau of Commercial Fisheries.

were chosen on the basis of water temperatures and are more meaningful in the present context than terrestrial seasons.

Seasonal Age Composition

James River

Catches in the James River (Table 1) typify the seasonal pattern observed in all three rivers. The age group that dominated July-September catches generally continued to dominate through the following June, i.e., for a complete sampling year that began in July.

Striped bass older than Age III were present throughout the 1967-1968 sampling year and were most abundant in spring. In other years, these mature fish appeared in April; some remained in the river through summer, but none were taken during the fall and winter. Young-of-the-year were generally absent from catches, except for the appearance of the 1969 year class in spring months of 1970.

York River

The general pattern of dominance observed in the James River was repeated in the York (Table 2). An exception occurred in winter months of 1970, when icing of the river severely reduced catches and the small sample consisted mostly of older fish. A more notable exception was the dominance of young-of-the-year striped bass in spring months of 1971.

Mature striped bass older than Age III rarely appeared during warmer months in the York River. Seventy-eight percent of these older individuals were taken in winter and spring months, 7.5% in the summer quarter.

Rappahannock River

Only one seasonal shift in age group dominance occurred in Rappahannock River catches of striped bass during the four-year sampling period. Older fish dominated in winter months of 1970 (Table 3), as observed in the York River.

TABLE 1.—Age composition of striped bass caught by nonselective fishing gear in the James River within quarterly periods, July 1967-June 1971.

Quarterly Period	Number in Age Group								
	0	I	II	III	IV	V	VI	≥VII	*N*
(1967) July-Sept	—	—	35	24	1	1	1	1	63
Oct-Dec	1	19	122	10	2	—	3	—	157
(1968) Jan-Mar	—	9	8	4	—	1	—	4	26
Apr-June	—	22	39	34	8	2	8	26	139
% Subtotal	0.3	13.0	53.0	18.7	2.9	1.0	3.1	8.1	
July-Sept	—	70	189	94	27	4	1	3	388
Oct-Dec	—	97	89	13	—	—	—	—	199
(1969) Jan-Mar	(no samples)								0
Apr-June	—	154	108	16	19	10	8	12	327
% Subtotal	0	35.1	42.2	13.5	5.0	1.5	1.0	1.6	
July-Sept	—	31	235	58	3	4	—	3	334
Oct-Dec	—	8	85	13	—	—	—	—	106
(1970) Jan-Mar	—	1	3	2		—	—	—	6
Apr-June	19	33	81	29	10	3	2	14	191
% Subtotal	3.0	11.5	63.4	16.0	2.0	1.1	0.3	2.2	
July-Sept	1	98	57	64	12	1	1	1	235
Oct-Dec	—	33	8	6	—	—	—	—	47
(1971) Jan-Mar	(no samples)								0
Apr-June	(no samples)								0
% Subtotal	0.4	46.5	23.0	24.8	4.3	0.4	0.4	0.4	
							Total Number Aged		2,218

TABLE 2.—Age composition of striped bass caught by nonselective fishing gear in the York River within quarterly periods, July 1967-June 1971.

Quarterly Period	Number in Age Goup								
	0	I	II	III	IV	V	VI	≥VII	*N*
(1967)									
July-Sept	—	317	22	4	—	—	—	—	343
Oct-Dec	—	112	20	1	—	—	—	—	133
(1968)									
Jan-Mar	—	16	13	11	—	—	—	—	40
Apr-June	2	119	21	2	—	—	—	2	146
% Subtotal	0.3	85.2	11.5	2.7	0	0	0	0.3	
July-Sept	—	84	126	5	—	1	—	2	218
Oct-Dec	1	274	210	27	4	—	—	—	516
(1969)									
Jan-Mar	1	178	151	40	14	4	1	1	390
Apr-June	11	191	75	15	3	3	1	6	305
% Subtotal	0.9	50.9	39.3	6.1	1.5	0.6	0.1	0.6	
July-Sept	—	221	149	13	2	2	—	—	387
Oct-Dec	8	225	200	47	11	2	1	3	497
(1970)									
Jan-Mar	—	1	4	6	1	—	—	—	12
Apr-June	41	84	33	10	2	3	2	—	175
% Subtotal	4.6	49.6	36.0	7.1	1.5	0.7	0.3	0.3	
July-Sept	—	223	48	2	—	—	—	—	273
Oct-Dec	13	425	65	16	6	—	—	—	525
(1971)									
Jan-Mar	13	82	13	8	1	1	—	3	121
Apr-June	145	131	9	12	7	—	2	2	308
%Subtotal	13.9	70.2	11.0	3.1	1.1	0.1	0.2	0.4	
								Total Number Aged	4,389

Seasonal occurrence of striped bass older than Age III was similar to that observed in the York. Eighty-three percent of these individuals were taken in winter and spring months, 11.2% in the summer months.

Young-of-the-year first appeared in fall catches, but significant numbers were not taken until the following spring. This seasonal pattern was similar to observations from the York River.

Differences in Age Composition between Years and Rivers

Differences between both years and rivers in the age structure of Virginia striped bass catches are shown in Figure 2, where age composition data have been combined into sampling year totals within river systems. James River catches were dominated by Age II striped bass in three of the four sampling years, and by Age I fish (1969 year class) in 1970-1971. Rappahannock River catches, on the other hand, were dominated by Age I striped bass in three of the four years, and by Age II fish in 1968-69. Age I fish dominated York River catches in all four years. Except for the continued domination of Rappahannock River catches by the 1966 year class during the 1968-69 sampling year, age composition in the York and Rappahannock rivers was similar.

Among the 1965-1969 year classes which progressed through the fishery as Age I and II fish during the four-year sampling period, the 1966 year class appears to have contributed most heavily to the York and Rappahannock river catches. The 1967 year class was strongest in the James River. Dominance of year classes in the various years and river systems is summarized in Table 4.

TABLE 3.—Age composition of striped bass caught by nonselective fishing gear in the Rappahannock River within quarterly periods, July 1967-June 1971.

Quarterly Period	Number in Age Group								
	0	I	II	III	IV	V	VI	≥VII	N
(1967) July-Sept	—	124	11	2	—	—	—	—	137
Oct-Dec	2	280	48	11	2	—	—	1	344
(1968) Jan-Mar	—	84	25	17	4	6	19	23	178
Apr-June	6	217	12	2	—	1	—	1	239
% Subtotal	0.9	78.5	10.7	3.6	0.7	0.8	2.1	2.8	
July-Sept	—	81	220	1	2	—	—	—	304
Oct-Dec	4	124	256	8	1	—	—	—	393
(1969) Jan-Mar	—	36	139	14	4	1	—	3	197
Apr-June	30	121	146	8	—	1	—	11	317
% Subtotal	2.8	29.9	62.8	2.6	0.6	0.2	0	1.2	
July-Sept	—	156	110	47	3	3	—	—	319
Oct-Dec	—	152	113	32	3	—	—	—	300
(1970) Jan-Mar	—	17	35	40	2	1	—	4	99
Apr-June	28	142	20	44	4	5	1	10	254
% Subtotal	2.9	48.0	28.6	16.8	1.2	0.9	0.1	1.4	
July-Sept	—	123	87	7	10	1	—	—	228
Oct-Dec	8	200	86	4	1	—	1	—	300
(1971) Jan-Mar	3	127	64	16	14	1	4	1	230
Apr-June	86	149	30	7	14	1	1	5	293
% Subtotal	9.2	57.0	25.4	3.2	3.7	0.3	0.6	0.6	
								Total Number Aged	4,132

DISCUSSION

Seasonal and Annual Age Composition of River Catches

Seasonal variation in the age composition of striped bass catches is slight (Tables 1-3) when viewed over a sampling year begun in July. Most of the seasonal variation occurs among subdominant age groups, specifically the appearance of young-of-the-year in the fall and the annual return of older, mature stocks in winter and spring. A year class that is dominant in summer tends to remain dominant through the following spring. Changes in year class dominance from one year to another usually occur in summer, so *age group* dominance tends to remain constant.

Annual differences in age composition, on the other hand, can be striking. Although Age I striped bass are expected to predominate in pound net and fyke net catches, strong year classes may continue to dominate catches a second year as Age II individuals. This occurred in the Rappahannock River as a result of the strong 1966 year class (Figure 2).

The predominance of Age II striped bass catches from the James River during three of the four sampling years differs from the age composition observed in the York and Rappahannock rivers. Partial explanations are available for two of these cases: 1) the 1965 year class dominated 1967-68 catches because of the local failure of the 1966 year class (Grant and Joseph, 1969); 2) the 1966 year class dominated 1968-1969 catches after entering the James from other rivers where it was an unusually successful year class.

The Virginia Fishery and Cycles of Abundance

The appearance of a dominant year class of striped bass in Chesapeake Bay waters is reflected in subsequent catches within the Bay

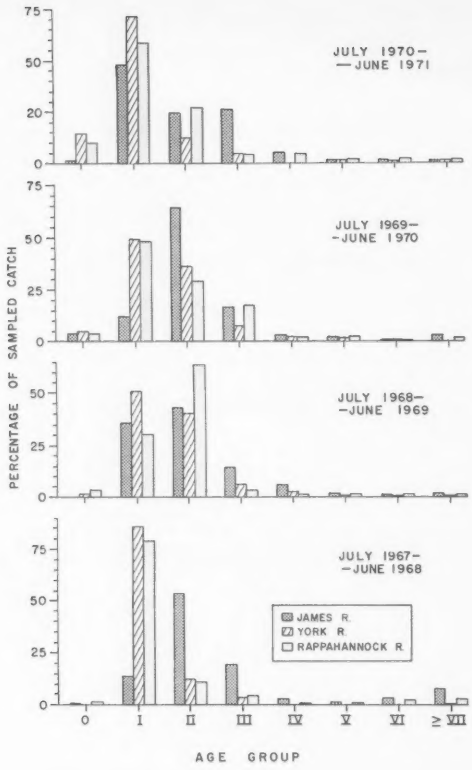

FIGURE 2.—Age composition of sampled pound and fyke net catches in the James, York, and Rappahannock rivers, July 1967-June 1971.

(Tiller, 1950; Vladykov and Wallace, 1952; Murphy, 1960; Shearer, Ritchie, and Frisbie, 1962) and along the migration route in coastal states from Virginia to New England (Merriman, 1941; Schaefer, 1968). Schaefer (1968) concluded that Chesapeake Bay is the primary source of striped bass caught in the surf of Long Island, and that Hudson River stocks may significantly contribute to these populations only when dominant year classes from Chesapeake Bay are unavailable. Yet it is generally believed, although still debatable, that only a small proportion of those striped bass originating in Chesapeake Bay enter the coastal migration (Vladykov and Wallace, 1952; Mansueti, 1961; Massmann and Pacheco, 1961; Grant et al., 1970).

Koo (1970) has shown an apparent six-year

TABLE 4.—Summary of the year classes of striped bass that dominated catches in Virginia rivers, 1967-1971.

River	Sampling Year (July through June)			
	1967-68	1968-69	1969-70	1970-71
James	1965	1966	1967	1969
York	1966	1967	1968	1969
Rappahannock	1966	1966	1968	1969

TABLE 5—Contribution of age groups I-III to pound net and fyke net catches of striped bass in three Virginia rivers, 1967-1971.

Sampling Year (July-June)	Percentage of Sampled Catch in Age Groups I-III		
	James	York	Rappahannock
1967-1968	84.7	99.4	92.8
1968-1969	90.8	96.3	95.3
1969-1970	90.9	92.7	93.4
1970-1971	94.3	84.3	85.6

cycle of abundance in Maryland. Such a cycle could result from the appearance of a dominant year class every six years, followed by three years of high catches (Ages I-III), then three of relatively low catches. The younger age groups (I to III) contribute most to Virginia pound net and fyke net catches of striped bass (Table 5), as expected for nonselective fishing gear. Over 90% of sampled individuals were from age groups I to III, except: 1) 84.7% in the James River during the first year of sampling due to catches of large numbers of older fish, particularly the 1958 year class; 2) 84.3% in the York River in the 1970-1971 sampling year; and 3) 85.6% in the Rappahannock River in the same year. The last two exceptions occurred because of contributions by the latest dominant year class (1970—then Age 0).

Although the age composition of Virginia catches would seem to conform to Koo's (1970) six-year cycle, no such cycle is apparent in Virginia landings (Figure 1), even though the dominant year classes mentioned by Koo (1970) were also successful ones in Virginia. The difference between Maryland and Virginia landings, relative to this six-year cycle, might stem from local successes of year classes interspersed among those appearing at six-year intervals. In addition to the 1958, 1964 and 1970 cyclically dominant year classes, certain Virginia rivers have produced large hatches of striped bass in 1961 and 1966 (Grant and Joseph, 1969; Grant, Burrell, and Kriete, 1971). Catches of these aperiodically strong year clas-

es tend to obscure, or even eliminate, peaks in landings contributed by Koo's Chesapeake-wide dominant year classes. Thus only long-term trends in abundance remain evident (Figure 1).

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LARVAL FISHES OF YAQUINA BAY, OREGON: A NURSERY GROUND FOR MARINE FISHES?

WILLIAM G. PEARCY AND SHARON S. MYERS[1]

ABSTRACT

Based on a survey of planktonic fish larvae, the Yaquina Bay estuary appears important as a spawning or rearing ground only for *Clupea harengus pallasi* (Pacific herring) and a variety of small cottids, gobies, and stichaeids. Other investigators, however, have found an abundance of juvenile *Parophrys vetulus* (English sole), *Citharichthys stigmaeus* (sanddab), *Hypomesus pretiosus* (surf smelt), *Platichthys stellatus* (starry flounder) and embiotocids (surf perches), indicating that the bay is an important nursery area for these species.

Of the 44 types of larval fishes found in the bay, *C. h. pallasi* and *Lepidogobius lepidus* (bay goby) were co-dominants each year, 1960-1970, comprising 90% of all larvae collected. There was no evidence of trends in abundances or species composition during the 11-yr study.

Maxima of planktonic fish eggs and *L. gobius* larvae occurred in the summer; maxima of all larvae combined and most species of larvae occurred in the winter and spring. High densities of larval herring were found in February and March, and peak numbers appeared earlier in the lower than the upper estuary.

Larvae of *C. h. pallasi, L. lepidus,* and *Cottus asper* were common at all stations from 0.5 to 8 nautical miles up the estuary, but not in the adjacent open ocean. Larvae of many species that were found in the estuary in small numbers were more abundant in offshore waters. Although English sole and sanddab were rare in the bay as larvae, juveniles were numerous.

This is a study of the species composition, relative abundance, seasonal and annual occurrence and distribution of larval fishes in an Oregon estuary. It was undertaken to increase the extremely limited knowledge of fish larvae in estuaries of the Pacific Northwest and to evaluate the role of these estuaries as spawning and nursery grounds.

According to Clark (1967) and McHugh (1966, 1967) the young of up to 70% of the economically important Atlantic species of fishes inhabit estuaries during part of their early life. Many species spawn offshore and young stages subsequently move into brackish estuaries. Although the Pacific coast is known for its runs of anadromous salmonids which migrate through estuaries, "There is no counterpart on the Pacific coast of the mass inshore movement of larvae and young of offshore-spawning nektonic species into brackish nursery grounds that is such a striking feature of the ecology of most Atlantic coast and Gulf of Mexico estuaries." (McHugh, 1967). Thus the number of species that are dependent on estuaries may not be as great on the Pacific as the Atlantic coast.

Oregon's estuaries are few in number and include but a small area. For this reason man's infringement on them for recreation, land development, harbors, agriculture, and waste disposal will be intense. This study evaluates some long-term trends of the relative abundance of larval fishes. Hopefully it will facilitate future comparisons of faunal changes within this estuarine habitat.

THE ESTUARY

Yaquina Bay (Figure 1) is a small tidal estuary on the central Oregon Coast. It extends inland about 37 km and has an area of about 11.6 km^2. A channel is dredged to a depth of 7.9 m to McLean Point and to 3.7 m to the town of Toledo. Tides are mixed, semidiurnal with a mean tidal range of 1.7 m (Kulm and Byrne, 1967). According to Zimmerman (1972) the bay has an exchange ratio of 52% and a flushing time of 13.3 tidal cycles during the summer. The estuary is well-mixed with little vertical stratification in the summer when freshwater runoff is low, and is partially mixed (4-19‰ salinity

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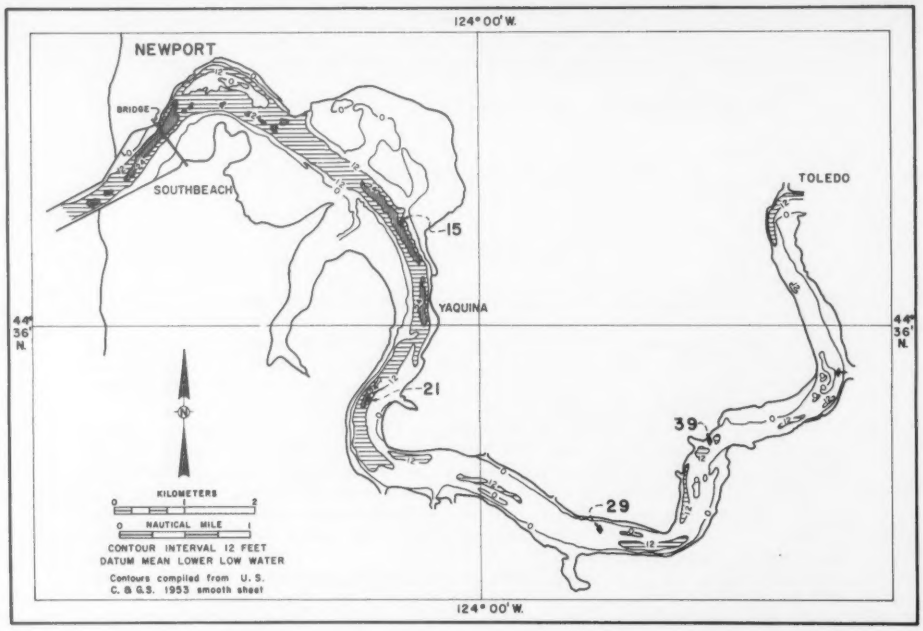

FIGURE 1.—Yaquina Bay estuary, showing location of stations: Bridge, Buoy 15, 21, 29, and 39.

difference from surface to bottom) during other seasons (Burt and McAlister, 1959; Kulm and Byrne, 1967; Zimmerman, 1972). Salinity is lowest and also most variable during the winter period of high precipitation. Temperatures, however, are most variable during the summer, owing to periodic advection of cold upwelled waters into the bay and to local heating (Frolander, 1964; Frolander et al., 1973).

SAMPLING METHODS

A 12.5 cm diameter Clarke-Bumpus (CB) Sampler with nylon (Nitex®)[2] net of 0.233 mm mesh aperture was used to collect 393 plankton samples from January 1960 to December 1970 and to provide a long time series for analysis at one station (Buoy 21) located in Yaquina Bay about 4.3 nautical miles from the ocean (Figure 1). In addition, both the CB and a 20.2 cm diameter nonclosing Bongo Sampler were towed together at five stations (Bridge and Buoys 15, 21, 29, and 39) from June 1969 to June 1970 (223 tows). The bongo had nylon nets with 0.233 mesh on one side and a 0.571 mesh on the other and was attached 1 m below the CB on the same towing cable. The CB net was 61.6 cm long with the filtering area of the mesh to mouth area ratio of 6.2:1. The bongo nets were cylindrical-conical, 177 and 161 cm long for the 0.233 and 0.571 mesh nets respectively. Both bongo nets had a filtering area to mouth area ratio of 10.5:1.

Samples were collected from small boats, generally at weekly intervals during the sampling period. Oblique-step tows were made at 2 knots. At the three deep stations (Bridge, Buoys 15 and 21) the net was towed horizontally at each of three depths for 4 min: about 1 m above the bottom, at mid-depth and 1 m below the surface. At the two shallow stations in the upper estuary the nets were towed at each of two depths for 6 min: 1 m above the bottom and 1 m below the surface. Tows were made during daylight, in mid-channel, against tidal currents, and did not coincide with any particular tidal stage. However, several 24-h series of CB tows (123 tows) were made during the 11-yr period to assess diel and tidal variations at single stations.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

Samples were also collected with the bongo nets (0.233 and 0.571 mm mesh) in the open ocean off Yaquina Bay from June 1969 to June 1970, often within a day of the bay sampling. A total of 113 step oblique tows was made at four stations 1, 3, 5, and 10 miles from the coast.

Volume of water filtered during each tow was estimated by flowmeters in the mouth of the nets. TSK meters were mounted on the inside wall of the bongo frames. Meters were calibrated periodically by towing them over a measured distance. Samples were preserved in the field with Formalin. In the laboratory entire samples were sorted for fish larvae with the aid of 2¼-power illuminated magnifier. Fish eggs were sorted from the 1960-1968 CB samples.

SPECIES COMPOSITION

Larval fishes representing 17 families were found in Yaquina Bay during the 11-yr studies. These included 45 distinct types of larvae, 22 of which were identified to species (Table 1). Most families were represented by only one or two species or types. The family Cottidae, however, was represented by 14 different larval types, by far the most for any family. The family with the next largest number of types was Pleuronectidae with 6 identified species.

TABLE 1.—Species composition of fish larvae from Yaquina Bay from all samples examined, 1960-1970.

Clupeidae
  Clupea harengus pallasi
Engraulidae
  Engraulis mordax
Osmeridae
  Hypomesus pretiosus
Gobiesocidae
  Gobiesox meandricus
Gadidae
  Microgadus proximus
Gasterosteidae
  Aulorhynchus flavidus
Syngnathidae
  Syngnathus griseolineatus
Stichaeidae
  Lumpenus sagitta
  Anoplarchus sp.
  Chirolophis sp.
  2 unknown types
Pholidae
  Pholis ornata
Ammodytidae
  Ammodytes hexapterus
Gobiidae
  Lepidogobius lepidus
  1 unknown type
Scorpanenidae
  Sebastes spp.
Hexagrammidae
  Hexagrammos sp.
  Ophiodon elongatus
Cottidae
  Leptocottus armatus
  Cottus asper
  Scorpaenichthys marmoratus
  Enophrys bison
  Hemilepidotus spp.
  9 unknown types
Agonidae
  2 unknown types
Cyclopteridae
  3 unknown types
Bothidae
  Citharichthys sp.
Pleuronectidae
  Psettichthys melanostictus
  Platichthys stellatus
  Glytocephalus zachirus
  Isopsetta isolepis
  Parophrys vetulus
  Lyopsetta exilis

THE 11-YR SERIES

Relative Abundances

Table 2 summarizes the occurrence and average density of different fish larvae collected during the 11-yr CB series at Buoy 21. Two species, *Clupea harengus pallasi* (Pacific herring) and *Lepidogobius lepidus* (bay goby), were clearly the most abundant larvae. Combined they accounted for 90% of all the fish larvae collected in the 393 samples.

These two species were consistently the co-dominants during all years of the sudy (Table 3). *C. h. pallasi* ranked first in abundance during 8 yr. *L. lepidus* ranked first in 3 yr and second in the 8 yr that *C. h. pallasi* was dominant. *Cottus asper* (prickly sculpin) ranked third in abundance. *Leptocottus armatus* (Pacific staghorn sculpin), Gobiidae type 1, and *Hypomesus pretiosus* (surf smelt) alternated in the fourth, fifth, and sixth positions. Average number of these larvae per m^3 varied from year to year, but no obvious long-term trends in the relative abundance of these species suggested environmental changes or species succession. (Similarly, Frolander et al. [in press] found no evidence for persistent changes of zooplankton abundances in Yaquina Bay over the same time period.)

In order to learn if all six of the common species were more abundant in some years than others, rank correlations were calculated from annual abundances in Table 3. *Clupea h. pallasi* and *L. lepidus* were both caught in large numbers in 1967, but the Coefficient of Concordance, W, (Tate and Clelland, 1957) indicated little agreement among ranking of years ($P > 0.2$). In other words, there was no

TABLE 2.—Fish larvae collected in Clarke-Bumpus nets during 1960-1970 at Buoy 21, ranked by abundance.

Item	No. of Tows occurred in out of 393	Total No. collected	Total No. larvae ÷ total volume of water filtered -- $m^3 \times 10^3$	Months of occurrence
Clupea harengus pallasi	76	2,174	510	I-V
Lepidogobius lepidus	98	1,287	302	IV-X
Cottus asper	47	129	30	I-V
Leptocottus armatus	42	53	12	VIII-III
Gobiidae type 1	27	49	11	VII-III, VI
Hypomesus pretiosus	23	39	9.1	VIII-IX, XI-IV
Lumpenus sagitta	8	29	6.8	I-II
Enophrys bison	12	20	4.7	I-III
Ammodytes hexapterus	10	15	3.5	I-III
Anoplarchus sp.	10	12	2.8	II-III
Cottidae type 1	8	10	2.3	II-III, VI-VII
Engraulis mordax	6	7	1.6	VII-IX
Pholis ornata	7	7	1.6	I-III
Parophrys vetulus	4	6	1.4	II-III
Platichthys stellatus	3	3	0.7	V-VI
Cyclopteridae type 1	3	3	0.7	VI, VII, XII
Cottidae type 10A	3	3	0.7	II, XI
Cottidae type 5	3	3	0.7	VIII, IX
Citharichthys sp.	2	2	0.5	II-III
Cyclopteridae type 2	2	2	0.5	VI-VII
Sygnathus griseolineatus	2	2	0.5	VII-VIII
Cottidae type 10B	1	1	0.2	I
Cottidae type 11	1	1	0.2	III
Sebastes spp.	1	1	0.2	I
Hexagrammidae	1	1	0.2	II

evidence that "good" or "bad" years occurred simultaneously for different species of larvae.

SEASONAL VARIATIONS

Total Eggs and Larvae

The average monthly catch of pelagic fish eggs at Buoy 21 was highest in the summer, with highest values ($>2/m^3$) from July to October (Figure 2). Eggs of the northern anchovy (*Engraulis mordax*) were sometimes abundant during this season. Numbers of fish larvae, on the other hand, peaked early in the year, from February to June, and few larvae were taken after June. *C. h. pallasi* and *L. lepidus* larvae were the main contributors to these large larval catches. These two species, and many others found in the estuary, have demersal eggs.

This seasonal maximum of fish larvae in the first half of the year in Yaquina Bay is similar to the seasonality reported in the Straits of Georgia, British Columbia by Parsons, LeBrasseur, and Barraclough (1970).

Individual Species

The seasonal occurrence of larvae collected at Buoy 21 is summarized in Table 2. The majority of the larval species were most common in the winter or spring, including *C. h. pallasi*, *Cottus asper*, *Hypomesus pretiosus*, *Parophrys vetulus*, *Ammodytes hexapterus*, *Lumpenus sagitta*, *Anoplarchus* sp., *Pholis ornata*, and *Enophrys bison*. *L. lepidus* was

TABLE 3.—Average abundance of the six most common fish larvae by year, 1960-1970, Clarke-Bumpus samples, Buoy 21.

Item	Average number of larvae per $10^3 m^3$ water filtered										
	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
Clupea harengus pallasi	174	542	278	279	1,230	335	273	1,136	961	526	506
Lepidogobius lepidus	312	230	37	114	326	402	161	1,169	471	74	132
Cottus asper	17	35	24	38	41	48	35	68	5	20	14
Gobiidae type 1	11	1	2	50	24	0	0	11	0	34	14
Leptocottus armatus	17	6	12	34	12	7	18	17	5	10	2
Hypomesus pretiosus	5	7	0	23	4	4	18	3	0	44	7

the only common species with a distinct peak of larval abundance in the summer (April-September). Several species were collected most months of the year: considering all years together, larvae of *Hypomesus pretiosus* were found every month but May, June, July and October, *L. armatus* every month except April-July, and Gobiidae type 1 every month but April, May and July.

Pacific Herring

Catches of *C. h. pallasi* larvae during each January-June period, 1960-1970, are illustrated for Buoy 21 in Figure 3. Herring larvae were common from February-April, with peak numbers usually in February and March. Though sampling variability and the limited number of samples precluded annual comparisons of abundance, no obvious long-term trends, such as decreasing catches, are evident during this 11-yr period, nor is there good evidence for large fluctuations in larval numbers. This suggests a fairly stable population of spawning herring over this time period.

The initial occurrence of larval herring varied among years, from January to March, suggesting annual differences in time of spawning or hatching times (e.g., contrast 1969 and 1970 with 1961-1963). This variability may be related to water temperature. The surface temperature of first larval occurrence varied from 7.3°C to 10.5°C (average = 9.0°C). To estimate date of first spawning, incubation time was calculated from a curve of incubation times vs. temperature (Outram, 1955; Taylor, 1971; Steinfeld, 1972). Incubation was estimated to range between 12 and 17 days for the first herring larvae caught during these years using surface water temperatures at Buoy 21. (Because herring spawn in shallow water, often intertidally [Steinfield, 1972; Taylor, 1971; Hardwick, 1973], surface temperatures were used.) Surface temperatures averaged for the date of first herring larval occurrence and the previous 17 days (2-3 observations) were plotted against time of first larval occurrence after January 1 (Figure 4). This revealed a surprising relationship: Years of earliest occurrence of larvae (i.e., 1969 and 1970) had lowest water temperatures (< 8°C) preceding first catches, and most years of latest occurrence (i.e. 1961, 1963, 1965, 1966) had highest temperatures (>9.2°C) during

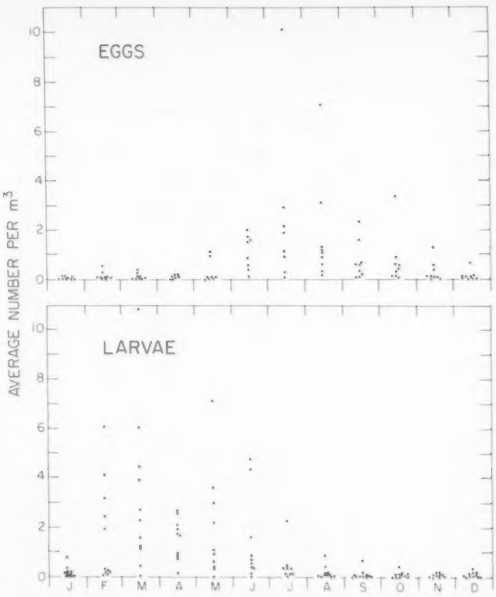

FIGURE 2.—Average monthly catches of fish eggs and larvae in Clarke-Bumpus samples at Buoy 21. Each point represents a monthly average for fish eggs each year, 1960-1968, and for fish larvae each year, 1969-1970. No samples were available from April-July 1966.

incubation of the first hatch. Thus, factors other than water temperature appear to be important in determining the time of the initial spawning of herring in Yaquina Bay.

Steinfeld (1972) observed from egg surveys in Yaquina Bay that herring had four major spawnings during February and March 1970. These occurred at about 2-wk intervals starting in early February, the most intensive spawnings coinciding with highest tides. Newly hatched larvae would therefore be expected in most of the catches throughout the larval periods. Measurements of larvae contributing to early and late peaks in 1964 and 1967 showed that recently hatched larvae (6-8 mm) were indeed present in April, but as expected, the percentage of small larvae was lower later in the year.

HORIZONTAL VARIATIONS

The average number of larvae collected at the different stations in both the estuary and the open ocean are listed in Table 4, permitting comparison of horizontal variations of relative abundance at nine stations from 8 miles up the

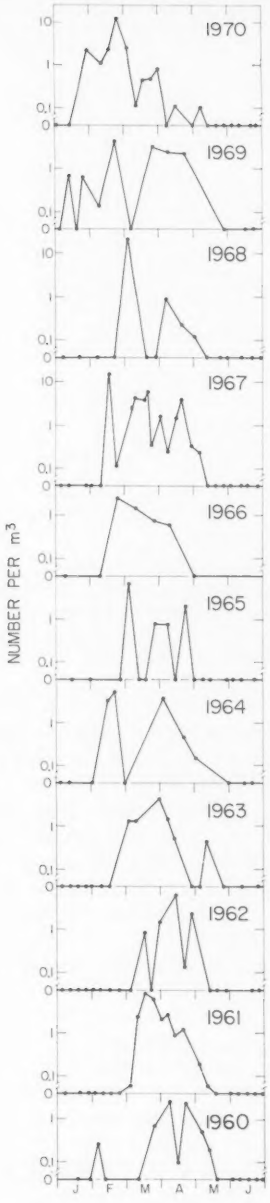

FIGURE 3.—Number of Pacific herring larvae per m³ caught in Clarke-Bumpus nets at Buoy 21 during January-June periods, 1960-1970.

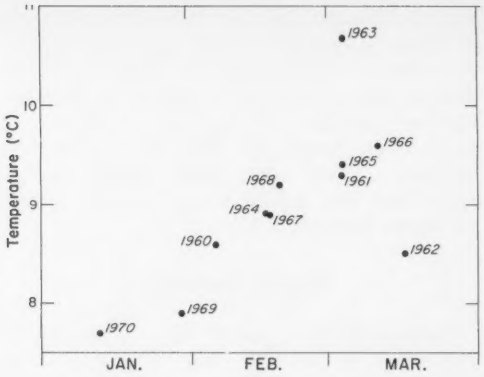

FIGURE 4.—Average surface temperature at Buoy 21 during and 14-17 days prior to first catches of herring larvae vs. date of first catches of herring larvae, 1960-1970.

estuary to 10 miles off the coast. Within the estuary, larvae of *C. h. pallasi*, *L. lepidus*, and *Cottus asper* usually ranked first, second, and third respectively in the catches at all five stations, from 0.5 to 8 nautical miles up the estuary. *L. lepidus* was the only common species restricted to the bay; it was most numerous in the upper estuary. Larvae of *C. h. pallasi* were abundant in the bay and rare outside the bay. Some of the other species that are considered to be primarily bay forms are *Cottus asper*, found in greatest numbers in the upper estuary, and *Enophrys bison*, *Leptocottus armatus* and *Pholis ornata*, found mainly in the lower estuary.

Many of the larvae found in the bay were found in greater numbers offshore. Larvae of the surf smelt, *H. pretiosus*, were sometimes abundant in the lower estuary where juvenile *H. pretiosus* were also numerous. Osmerids were most abundant 1 mile offshore. We assume that these were mainly *H. pretiosus*, a species known to spawn in the surf zone. Consequently, the surf smelt larvae found in the bay may be carried there by tidal exchange. Larvae of *A. hexapterus*, *Sebastes* spp., pleuronectids, gadids, and cyclopterids were all found in higher numbers offshore than in the bay. *Parophrys vetulus* was only found offshore.

Engraulis mordax larvae were found throughout the bay and to 3 miles offshore. They were not found 5 or 10 miles offshore. This larval distribution, and the large numbers of anchovy

TABLE 4.—Average number of larvae per $10^3 m^3$ filtered in bongo nets (mesh 0.233 and 0.571 mm combined) calculated from total number of specimens collected ÷ total volume filtered for entire year. Only species represented by five or more larvae are listed. June 1969-June 1970.

	BAY					OFFSHORE (mi)			
	39	29	21	15	BR	1	3	5	10
A. BAY ONLY									
Lepidogobius lepidus	106.0	340.5	113.4	92.9	6.4	0	0	0	0
Lumpenus sagitta	0	0	0.5	1.1	1.3	0	0	0	0
Anoplarchus spp.	0	0.6	0.7	1.1	1.0	0	0	0	0
B. PRIMARILY BAY									
Clupea h. pallasi	509.2	428.2	442.6	556.0	183.3	0.3	0.5	0	0
Gobiidae type 1	0.5	0.9	13.7	5.3	1.3	0.6	0.3	0	0
Cottus asper	40.7	42.3	21.0	10.1	9.2	0.6	0	0	0
Enophrys bison	0	0	2.3	9.6	18.8	0.3	0	0	0
Leptocottus armatus	0.7	1.6	10.0	7.2	3.8	0.3	0	0	0
Cottidae Type 1	0	0	0.5	1.3	1.3	0.6	0.5	1.0	0.3
Pholis ornata	0	0	0.8	1.3	1.3	0.3	0.5	0	0
C. PRIMARILY OFFSHORE									
Engraulis mordax	0.5	1.0	0.5	0.3	0.2	2.1	1.1	0	0
Hypomesus pretiosus-Osmerids	1.0	0.6	3.0	15.7	27.2	100.9	18.6	4.6	0.3
Gadidae	0	0	0.5	0	0.2	0.6	4.5	0.7	1.1
Ammodytes hexapterus	0	0	0	0.5	0.5	1.8	13.0	2.0	2.5
Sebastes spp.	0	0	0	0.5	0.8	6.9	4.2	1.5	19.6
Ophiodon elongatus	0	0	0	0.3	0	0.6	0.8	0.7	0
Hemilepidotus	0	0	0	0	0.2	1.5	2.9	0	1.2
Cottidae type 12	0	0	0	0.3	0.5	0.9	0	0	0
Agonidae	0	0	0	0	1.0	0.3	0.5	0.2	0
Cyclopteridae	0	0	0.2	0.3	0.2	0.6	3.2	0.2	0.5
Psettichthys melanostictus	0.2	0	0.5	0	0.5	5.1	31.1	3.4	0.5
Isopsetta isolepis	0	0	0	0	0.2	0.6	36.1	5.1	1.1
Lyopsetta exilis	0.2	0	0	0	0	0	9.0	0	0.3
Citharichthys sp.	0	0	0	0.5	0.5	1.0	0	0	0
D. OFFSHORE ONLY									
Stenobrachius leucopsarus	0	0	0	0	0	0.3	0.5	1.0	1.6
Cottidae type 16	0	0	0	0	0	0	2.4	0	0.3
Cottidae unident. spp.	0	0	0	0	0	1.8	9.6	7.1	0.6
Parophrys vetulus	0	0	0	0	0	1.2	9.0	11.9	8.9
Blennoids	0	0	0	0	0	3.3	4.5	0	0

eggs within the bay, is peculiar since Richardson (1973) reported that anchovy larvae were abundant well offshore, usually in Columbia River plume waters, and not near the coast.

Pacific Herring

Abundance

Herring larvae were abundant at all five stations during February and March 1970 (Figure 5). A peak in catches occurred in late January at the three stations closest to the ocean, and conversely, higher numbers occurred later (April and May) at the upper estuarine stations. These trends suggest earlier spawning near the mouth and later spawning in the upper estuary. Based on intertidal surveys, Steinfeld (1972) found herring eggs near the mouth from February 5 to 20, 1970, and in the upper estuary above Buoy 21 from March 8 to 24, 1970. The trend for earlier spawning near the mouth of the estuary was therefore found in both larval and egg surveys. However, the fact that Steinfeld did not find any spawn before February 5 while we collected many larvae between January 23 and February 10 indicates that intertidal surveys may miss substantial areas of eggs, perhaps from subtidal spawning.

Comparison of Nets

Catches of herring larvae in the three types of nets (CB and bongo with 0.233 mm mesh and bongo with 0.571 mm mesh) were usually similar on a m^3 basis, especially at high densities of larvae (Figure 5). The type of net catching the highest or the lowest number of larvae alternated among tows. We had not expected catches by the CB to compare favorably with the bongo in view of the known avoidance capability of Atlantic herring larvae (Bridger, 1956; Tibbo et al., 1958).

The percentage of herring larvae of different

sizes caught at Buoy 29 in the three nets during the 1970 larval season is shown in Figure 6. Little difference is apparent in the proportion of different sizes of larvae in the different nets. All curves show that the number of larvae caught between 6 and 8 mm was less than between 8 and 10 mm. This is probably explained by hatching of some larvae at lengths over 8 mm, and hence is a true reflection of relative abundance, rather than lack of retention of the smallest larvae by the nets. Larvae larger than 20 mm were not caught at all in the CB samples, presumably because of the capability of large larvae to avoid this gear.

TIDAL-DIEL VARIATIONS

Figure 7 illustrates the variations in CB catches of fish eggs and larvae during several diel sampling periods at Buoy 21. In Figure 7A, peaks in both egg and larval abundance occurred during periods of low water (Mann-Whitney U test, $P < 0.01$). Similarly, highest catches of herring larvae coincided with times of low water in Figure 7B ($P = 0.06$). In neither of these figures is a day-night difference evident ($P > 0.2$). In Figure 7C, however, catches of herring larvae were not correlated with tidal stage ($P > 0.2$), but highest catches coincided with darkness ($P < 0.01$); all but one of the 9 nighttime catches exceeded the 14 daytime catches.

Therefore, both tidal and diel factors may influence catches. We believe the high catches associated with low water were caused by tidal excursion of water with high density of eggs or larvae. In other words, the center of abundance of *L. lepidus* larvae and fish eggs (Figure 7A) and *C. h. pallasi* (Figure 7B) was up the estuary from Buoy 21 at high tide. The ability of larger larvae to avoid plankton nets during the daytime (see Figure 6; Tibbo et al., 1958; Bridger, 1956; and Colton, Honey, and Temple, 1961) was thought to explain the high catches after dark in Figure 7C, but this interpretation was not supported by the similar size-frequency distributions of day- and night-caught larvae.

THE ESTUARY AS A NURSERY

The results of this study on the planktonic fish larvae tentatively support McHugh's (1966,

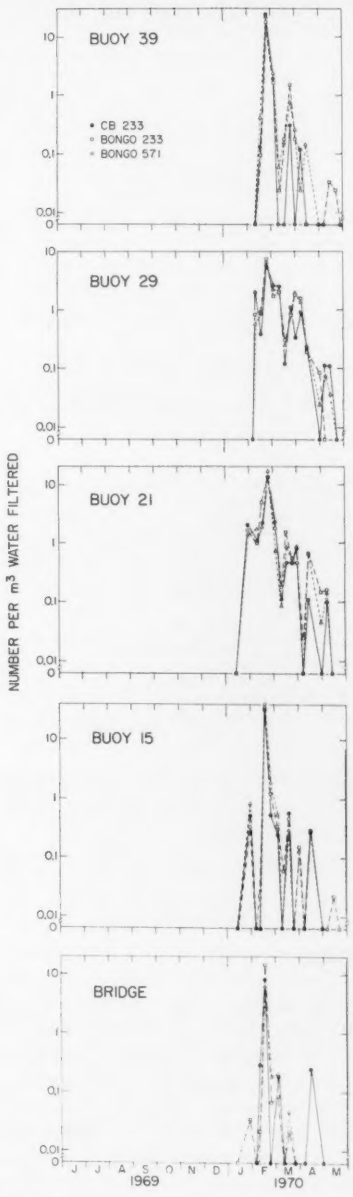

FIGURE 5.—Number of Pacific herring per m³ caught in Clarke-Bumpus nets with 0.233 mm mesh, the bongo net with 0.233 mm mesh and the bongo net with 0.571 mm mesh at five stations in Yaquina Bay, June 1969-June 1970.

1967) contention that estuaries of the Pacific coast may be less important as nursery grounds than eastern seaboard estuaries. But such a conclusion is unwarranted without a comparison of larval abundances within the estuary with those in adjoining open ocean to learn if larvae are restricted to or concentrated in estuaries. High numbers of larvae within the estuary are not necessarily proof of estuarine dependance, as they may be more abundant in the ocean. Conversely, low densities of a species inside the estuary may indicate importance if it is absent elsewhere. A comparison of larval catches in Yaquina Bay with the open ocean is possible since we collected fish larvae at stations 1, 3, 5, and 10 miles off Yaquina Bay, using the same bongo nets during the same sampling period as the bay sampling. The results of this comparison (Table 4) corroborate our earlier suggestion: with the exception of the Pacific herring the estuary does not appear to be important to the pelagic larvae of commercial fishes. Most of the larvae that were restricted to or were most common in the estuary were of small, non-food species of cottids, stichaeids, and gobies. Larvae of all the pleuronectids collected were more common offshore than inside the estuary.

Thus the Pacific herring was the only species of commercial interest that appeared to use the estuary extensively as both a spawning and a nursery ground. In California, herring spawn in bays and estuaries (Hardwick, 1973). Since Pacific herring are known to comprise more or less distinct populations with adults returning to the same bay to spawn (Stevenson, 1955; Rounsefell, 1930), estuaries may be vital to the maintenance of herring along some portions of the west coast.

Feeding conditions for herring are undoubtedly related to their use of estuaries as nurseries. Russell (1964) found that Yaquina Bay is used as a feeding ground for 1 to 4 yr-old herring which fed mainly on the copepods *Acartia clausii* and *Pseudocalanus* sp., both abundant within the bay. *A. clausii*, which is thought to maintain indigenous populations in Yaquina Bay, is especially abundant in the upper estuary (Buoys 21 and 29) early in the spring when densities of adults and immatures exceed 30,000m^3 (Zimmerman, 1972 Frolander et al., 1973). The numbers of copepod eggs, nauplii, and copepodites, important food for Atlantic herring larvae, probably exceed this

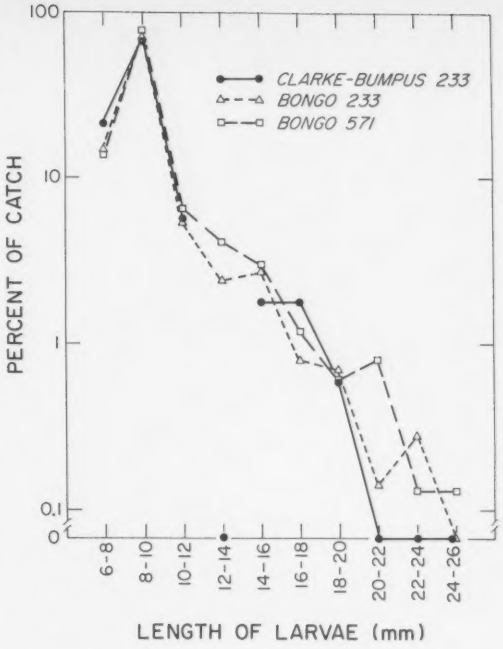

FIGURE 6.— Catches of different lengths of herring larvae at Buoy 29 expressed as a percentage of the total catch for each of the Clarke-Bumpus and bongo nets with 0.233 mm mesh and the bongo net with 0.571 mm mesh, February 10-March 13, 1970.

density during the early spring and provide adequate food for larval herring (Blaxter, 1965; Bainbridge and Forsyth, 1971; Sherman and Honey, 1971).

Our planktonic survey of fish larvae was not adequate to assess completely the estuary as a nursery ground. First, plankton nets are selective and only weakly swimming pelagic larvae were effectively sampled. Other young stages may not have been fully susceptible to capture because they actively avoid the nets. Secondly, the young of some species may have been present but simply unavailable for sampling because of their distributions. These may include young that migrate into the estuary after metamorphosis, benthic forms, or young that reside in shallow areas of the estuary.

For example, viviparous embiotocids (*Phanerodon furcatus*, *Rhacochilus vacca*, and *Embiotoca lateralis*) are common species in Yaquina Bay. Mature females of all these species are numerous in the middle and upper estuary

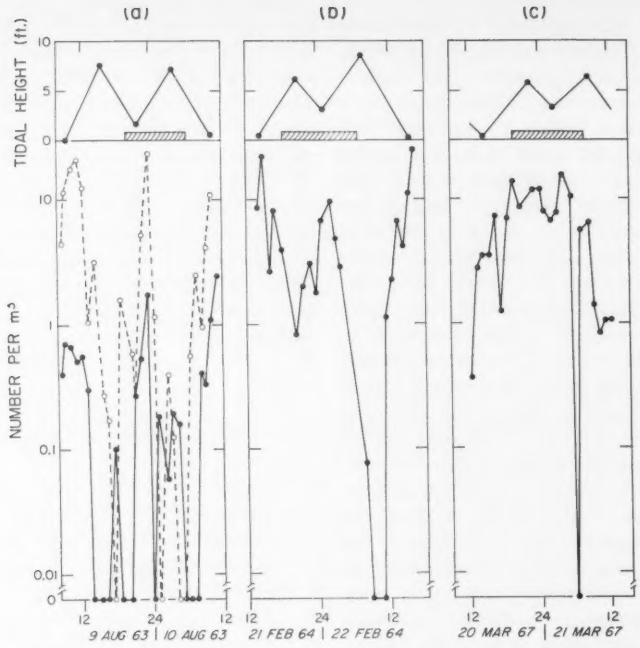

FIGURE 7.—Diel variations in the CB catches at Buoy 21: A. 9-10 August 1963; solid line = fish larvae; dashed line = fish eggs. B. 21-22 February 1964; solid line = herring larvae. C. 20-21 March 1967; solid line = herring larvae. The tidal height above mean lower-low water and period of darkness (hatched bar) are shown above each figure. Dates and noon and midnight are indicated below each figure.

during the spring when they give birth to young which use the estuary as a nursery (Beardsley, 1969; Wares, 1971). Because of their pelagic nature and swimming abilities, young embiotocids are not readily captured in small plankton nets or trawls. Beardsley (1969) and Westrheim (1955) also found many juvenile starry flounder (*Platichthys stellatus*) in Yaquina Bay, and Haertel and Osterberg (1967) concluded that the starry flounder use the upper Columbia River estuary as a nursery ground.

A trawl survey of juvenile fishes of Yaquina Bay by Wm. Johnson (pers. comm.), conducted during the same period and at the same stations as our plankton survey, provided useful information on the juvenile fishes caught in midchannel of the estuary near the bottom. Relative abundances of the young fishes caught are shown in Table 5. Three species were dominant: *Hypomesus pretiosus*, *Parophrys vetulus*, and *Citharichthys stigmaeus*. They comprised 79% of the total number of fishes collected. Of these, only the abundant *H. pretiosus* was also common in plankton collections (Tables 2, 3, and 4). *Lepidogobius lepidus*, *Cottus asper*, and *Leptocottus armatus*, though presumbly benthic as juveniles, were not abundant in the trawl collections despite their abundance as pelagic larvae. Johnson (pers. comm.) caught large numbers of juvenile *L. armatus* in shoal areas of Yaquina Bay with a beach seine, indicating that juveniles of some species may reside mainly in shallow water.

Young of both *Parophrys vetulus* and *Citharichthys stigmaeus* were abundant within Yaquina Bay, indicating that the bay provides a nursery for these species. Peak numbers of *P. vetulus* (15-45 mm) were found between April and June at Buoy 21, but young were captured at all stations from Buoy 15 to 39.

Citharichthys stigmaeus (30-80 mm) were concentrated in the lower estuary and were rarely captured up-estuary of Buoy 21. They were most common in May and June. *Hypomesus pretiosus* (35-50 mm) were abundant at all trawling stations, but only in January and February (Johnson, pers. comm.).

The importance of estuaries as nursery grounds for flounder, and especially for *Parophrys vetulus*, has been emphasized by others. Westrheim (1955) reported appreciable numbers of small *Parophrys vetulus*, *Citharichthys sordidus*[3] and *Platichthys stellatus* (starry flounder) in Yaquina Bay. Sand sole (*Psettichthys melanostictus*) were also encountered frequently. Although no adults of the commercially important English sole were caught, juveniles (20-180 mm) were common until autumn when most emigrated from the bay. Olsen and Pratt (1973) also reported that juvenile English sole were abundant in lower Yaquina Bay from April to September 1971, emigrating to offshore areas in October. Based on the incidence of a parasitic infection, apparently acquired only in estuaries, they concluded that estuaries are likely to be the exclusive nursery grounds for *Parophrys vetulus* on the Oregon coast, a conclusion that is supported by the absence of 0-age English sole in Demory's (1971) ocean trawling survey off the Oregon-Washington coast. Misitano (1970) and Eldridge (1970) found large numbers of English sole in Humboldt Bay, California. Villadolid (1927, as cited in Misitano, 1970) captured 0-age English sole by trawling in San Francisco Bay but found none off the coast. Shallow protected waters along the indented British Columbia coastline also provide nursery grounds for this species (Ketchen, 1956). Bays and estuaries are therefore vital as nursery areas for *P. vetulus* in their first year of life, perhaps because the sediments in these protected waters provide an ideal feeding habitat for the young as opposed to coarse sand sediments at similar depths along the open coast.

Sexually mature (ripe) *P. vetulus* were not caught in Humboldt or Yaquina Bay but are known to spawn offshore (Westrheim, 1955; Harry, 1959; Jow, 1969). Young larvae were uncommon in plankton collections from these bays (Eldridge, 1970; Misitano, 1970). In our study *P. vetulus* larvae were common offshore but were absent or rare in Yaquina Bay (Table 4). Therefore young English sole must be transported into the bay from offshore waters as late larval stages or migrate in as juveniles. In Humboldt Bay, Misitano (1970) captured metamorphosing English sole (average length, 23 mm) by midwater trawling, especially after dark. These larvae were active swimmers in aquaria but usually resided on the bottom. As a result they would be relatively inaccessible to daytime plankton collections.

The question remains, however, how these larvae enter estuaries. Currents off the northern Pacific coast during the winter and spring are largely inshore and northerly (Burt and Wyatt, 1964; Wyatt, Burt, and Pattullo, 1972) and would transport buoyant fish eggs such as those of English sole (Budd, 1940; Ketchen, 1956; Alderdice and Forrester, 1968) toward and then along the coast. Retention in estuaries would seem to require active behaviorial responses by the larvae, such as a change in depth distribution to enhance transport into and reduce advection out of estuaries. Since a two-layered transport system prevails in Yaquina Bay during the winter (Kulm and Byrne, 1967; Burt

TABLE 5.—Relative abundance (%) of juvenile fishes collected at four stations in Yaquina Bay (Bridge to Buoy 29) in a 1.8-m beam trawl (1.5 mm stretch mesh), January-June, 1970 (courtesy Wm. Johnson).

Hypomesus pretiosus	36.2
Parophrys vetulus	24.6
Citharichthys stigmaeus	18.2
Enophrys bison	4.1
Clupea h. pallasi	3.6
Ammodytes hexapterus	2.5
Leptocottus armatus	2.3
Hexagrammos decagrammus	1.1
Pholis ornata	1.0
Raja binoculata	0.7
Platichthys stellatus	0.7
Hemilepidotus hemilepidotus	0.7
Lumpenus sagitta	0.7
Engraulis mordax	0.6
Lepidogobius lepidus	0.5
Cymatogaster aggregata	0.5
Sebastes melanops	0.4
Artedius fenestralis	0.4
Psettichthys melanostictus	0.4
Ophiodon elongatus	0.3
Sygnathus griseolineatus	0.3
Pallasina barbata	0.1
Symphurus atricauda	<0.1
Artedius harringtoni	<0.1
Anoplarchus purpurescens	<0.1
Phanerodon furcatus	<0.1
Embiotoca lateralis	<0.1
Occella verrucosa	<0.1
Gobiesox maeandricus	<0.1

[3] Probably *C. stigmaeus*, the species usually found by others in Yaquina Bay.

and McAlister, 1959) and since Kulm and Byrne (1967) found that marine sand was transported by strong currents 6 miles up the Yaquina Bay estuary during the winter, the season when *P. vetulus* enter the estuary, then descent of larvae into deep water, where net transport exists up the estuary, may result in transport into and retention within estuaries of English sole and other species, as found for other larval fish (Pearcy, 1960; Pearcy and Richards, 1962; and Graham, 1972).

In conclusion, Yaquina Bay, like many east coast estuaries, is an important nursery for the young of several species of marine fishes. This was not apparent from a survey of planktonic larvae, however. Only the larvae of Pacific herring, a species that spawns in bays, were abundant in our plankton collections in Yaquina Bay. Although the pelagic larvae of flatfishes were much more common in offshore than estuarine waters, the juveniles of several species move into the estuary in large numbers.

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CALANOID COPEPODS OF THE GENUS *AETIDEUS* FROM THE GULF OF MEXICO[1]

TAISOO PARK[2]

ABSTRACT

The copepod population known previously as belonging to *Aetideus armatus* (Boeck) in the Gulf of Mexico and Caribbean Sea is recognized as a separate species. The males of *Aetideus acutus* Farran and *Aetideus giesbrechti* Cleve are fully redescribed with figures.

The genus *Aetideus* Brady, 1883, comprised four species (*A. armatus*, *A. bradyi*, *A. acutus*, and *A. giesbrechti*) when Sars (1925) established the genus *Euaetideus* to distinguish the last three species from the first. A new species has since been added to each genus, *A. pacificus* and *E. australis*. Bradford (1971) reviewed the genera *Aetideus* and *Euaetideus* on the basis of specimens from the Atlantic and Pacific Oceans. Having found a close similarity between the males, she proposed the merging of the two genera. In agreement with her proposal, the name *Euaetideus* is considered here as a junior synonym of *Aetideus*.

In the Gulf of Mexico, three species of *Aetideus* (*A. armatus*, *A. acutus*, and *A. giesbrechti*) have been recorded (Owre and Foyo, 1967; Park, 1970). During the examination of plankton samples obtained from the Gulf of Mexico by the RV *Alaminos* in September 1971, all of these species were found, including the males.

A. armatus had been known to have worldwide distribution (Vervoort, 1957) until Bradford (1971) recognized a population in the Southern Hemisphere and two in the North Pacific as separate species. Bradford also noted differences between the northern and southern forms of *A. armatus* in the Atlantic, but the differences were not considered as taxonomically significant. When examined in detail in the light of Bradford's findings, the Gulf of Mexico population of *A. armatus*, however, was found to be significantly different from either the northern or southern Atlantic form of the species, or from any other known species of the genus. Therefore, it is described here as a new species.

A. acutus and *A. giesbrechti* found in this study were in agreement with the descriptions by Grice (1962) and Park (1968) for the Pacific forms. The males of these species have not been fully described, except for brief descriptions by Giesbrecht (1892) and Bradford (1971).

AETIDEUS MEXICANUS, NEW SPECIES

Type.—Holotype female, U.S. National Museum No. 143777; allotype male USNM No. 143778; 30 female and 7 male paratypes, USNM No. 143779. Type locality, lat. 25°15'N, long. 89°11'W, in the Gulf of Mexico (sampling depth, about 500-0 m).

Female.—Body lengths of 31 type specimens, 1.66-1.84 mm. Proportional lengths of prosome and urosome about 78:22. Viewed dorsally, body slender, with a round, slightly produced forehead (Figure 1A). Laterally, dorsal margin of forehead broadly vaulted at level of mouth (Figures 1B, D). Two rostral rami separated by a U-shaped notch (Figure 1G). Distance between tips of rostral rami exceeding depth of notch (1.07-1.15:1). Metasomal process extending straight backward; although variable in length, generally reaching about distal end of genital segment. Dorsally, genital segment (Figure 1H) wider than long, with its widest part close to its proximal end. Shape of spermatheca (Figures 1C, F) similar to *A. armatus* as described by Bradford (1971), with short wide neck connecting proximal and distal sacs; space between two sacs slightly

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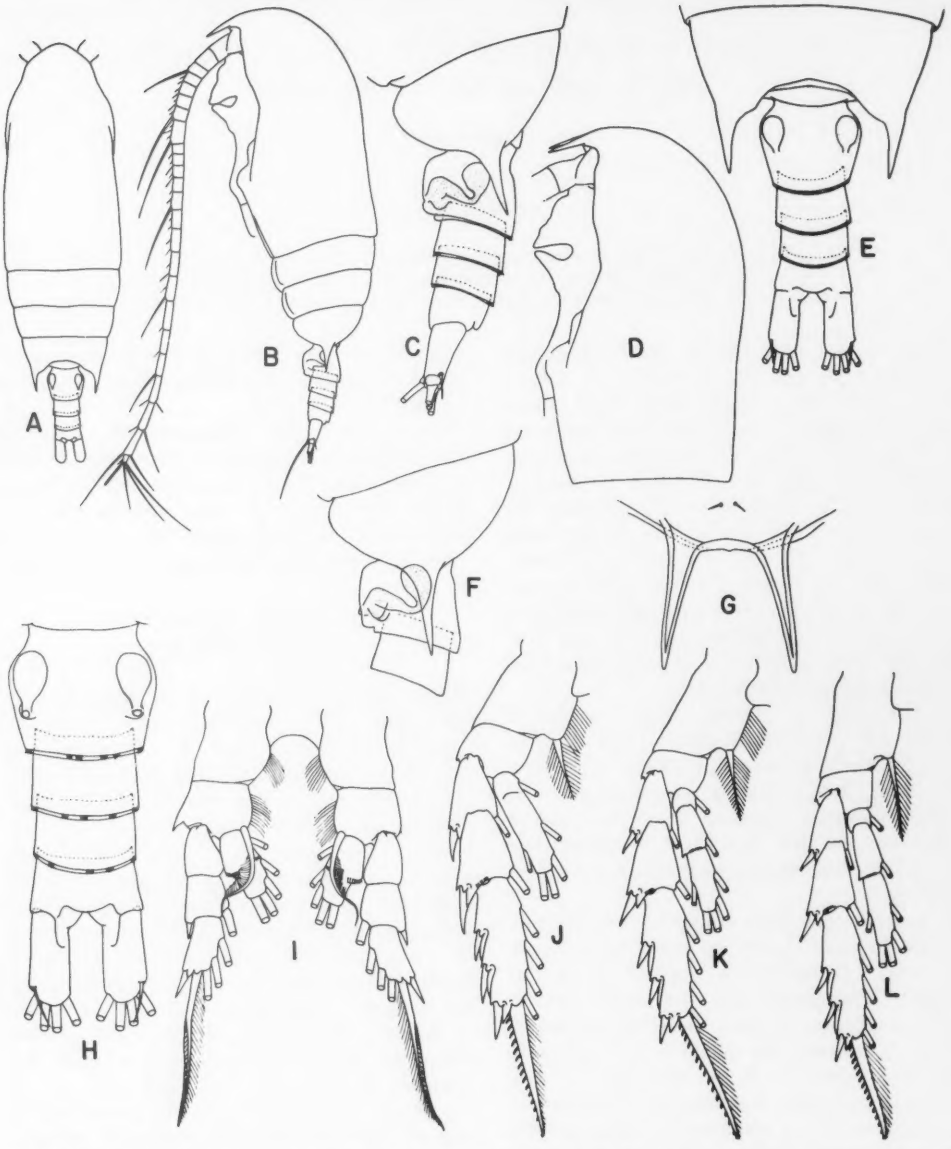

FIGURE 1.—*Actideus mexicanus*, new species. Female: A, habitus, dorsal; B, habitus, lateral; C, posterior part of body, lateral; D, forehead, lateral; E, posterior part of body, dorsal; F, last metasomal and first two urosomal segments of another specimen, lateral; G, rostrum, anterior; H, urosome, dorsal; I, first pair of legs, anterior; J, second leg, anterior; K, third leg, anterior; L, fourth leg, anterior.

wider than connecting neck. Caudal ramus about 2.4 times as long as wide.

Antennules extending beyond distal end of caudal ramus by last two segments. Other cephalic appendages as in *A. pacificus* as described by Park (1968). In most of the specimens dissected the first pair of legs were asymmetrical, with the external margin of the right

basis produced distally into a large tooth-like process (Figure 1I). Second to fourth legs (Figures 1J-L) similar to *A. pacificus*, but coxa of fourth leg without spinules at base of internal seta. Terminal exopodal spines of second to fourth legs with 15-17 teeth.

Male.—Body lengths of eight type specimens, 1.58-1.68 mm. Proportional lengths of prosome and urosome about 75:25. Body slender, with forehead slightly produced (Figure 2A). Rostrum reduced. Metasomal process pointing straight backward, reaching about distal end of genital segment (Figures 2D, E). Second to fourth urosomal segments and caudal rami (Figure 2E) with width:length ratios of 1:0.98-1.05, 1:1.08-1.15, 1:1.12-1.19, and 1:1.82-2.00, respectively. Antennules reaching about distal end of fourth urosomal segment, nineteenth and longest segment (Figure 2G) with width:length ratio of 1:4.9-5.1. On second leg (Figure 2M), endopod reaching distal end of second exopodal segment. On second and third legs (Figure 2N), terminal exopodal spines longer than third exopodal segments, with about 29 and 23 teeth, respectively. Second to fourth segments of fifth leg (Figure 2O) with width:length ratios of 1:3.7-4.2, 1:8.3-8.7, and 1:9.0-9.7, respectively.

Remarks.—The female of *A. mexicanus* is distinguished from *A. armatus* by the slender body, long antennules which extend beyond the caudal rami by two segments and, particularly, the fourth leg which lacks spinules at the base of the coxal seta found in all other species of the genus (Bradford, 1971). The male of *A. mexicanus* is very close to that of *A. armatus* as described by Bradford but seems to differ from it in the proportions of the caudal rami and of the second to fourth segments of the fifth legs. However, the importance of these characters in the distinction between the two species is yet to be determined.

Distribution.—*A. mexicanus* was found in a number of plankton samples taken from the upper 500 m in the Gulf of Mexico by the RV *Alaminos* in September 1971. *A. armatus* recorded from the Caribbean Sea by Park (1970) belongs to this new species.

AETIDEUS ACUTUS FARRAN, 1929

Male.—Body length, 1.22-1.36 mm according to 48 randomly selected specimens. Proportional lengths of prosome and urosome about 79:21. Dorsally, forehead (Figure 3B) more produced than in *A. mexicanus*. Rostrum reduced. Metasomal process with wide base, distinctly curved downward when viewed laterally (Figure 3E) and slightly curved inward in dorsal view (Figure 3D). Second to fourth urosomal segments and caudal rami with width: length ratios of 1:0.83-0.88, 1:0.75-0.81, 1:0.78-0.81, and 1:1.64-1.83, respectively.

Antennules reaching about distal end of third urosomal segment, nineteenth and longest segment (Figure 3F) with width:length ratio of 1:3.31-3.52. Other cephalic appendages similar to *A. mexicanus*. On second leg (Figure 3L), endopod reaching distal end of second exopodal segment. Terminal exopodal spines of second and third legs (Figure 3M) longer than their third exopodal segments, with about 23 and 18 teeth, respectively. Terminal exopodal spines of fourth legs (Figure 3N) shorter than their third exopodal segments, with about 16 teeth. Second to fourth segments of fifth leg (Figure 3O) with width:length ratios of 1:3.41-3.78, 1:6.72-7.33, and 1:6.00-6.60, respectively.

Remarks.—The male of *A. acutus* was first described very briefly by Bradford (1971). The present specimens seem to be in agreement with her descriptions. The male of *A. acutus* is easily distinguished from those of *A. mexicanus* and *A. giesbrechti* by its considerably smaller size. In the shape of the forehead, metasomal process, and antennule, it is closely related to *A. giesbrechti*, but differs from this species in the relative lengths of the urosomal segments and caudal rami.

The female specimens of *A. acutus* in the present study (1.48-1.62 mm in body length according to 80 randomly selected specimens) are identical with the specimens described by Park (1968) from the Pacific, and can be readily recognized by the shape of the spermatheca (Figure 3A). The appendages are similar to those of *A. pacificus* as described by Park (1968), except that the maxillule carries 3+3+6 setae on the endopod.

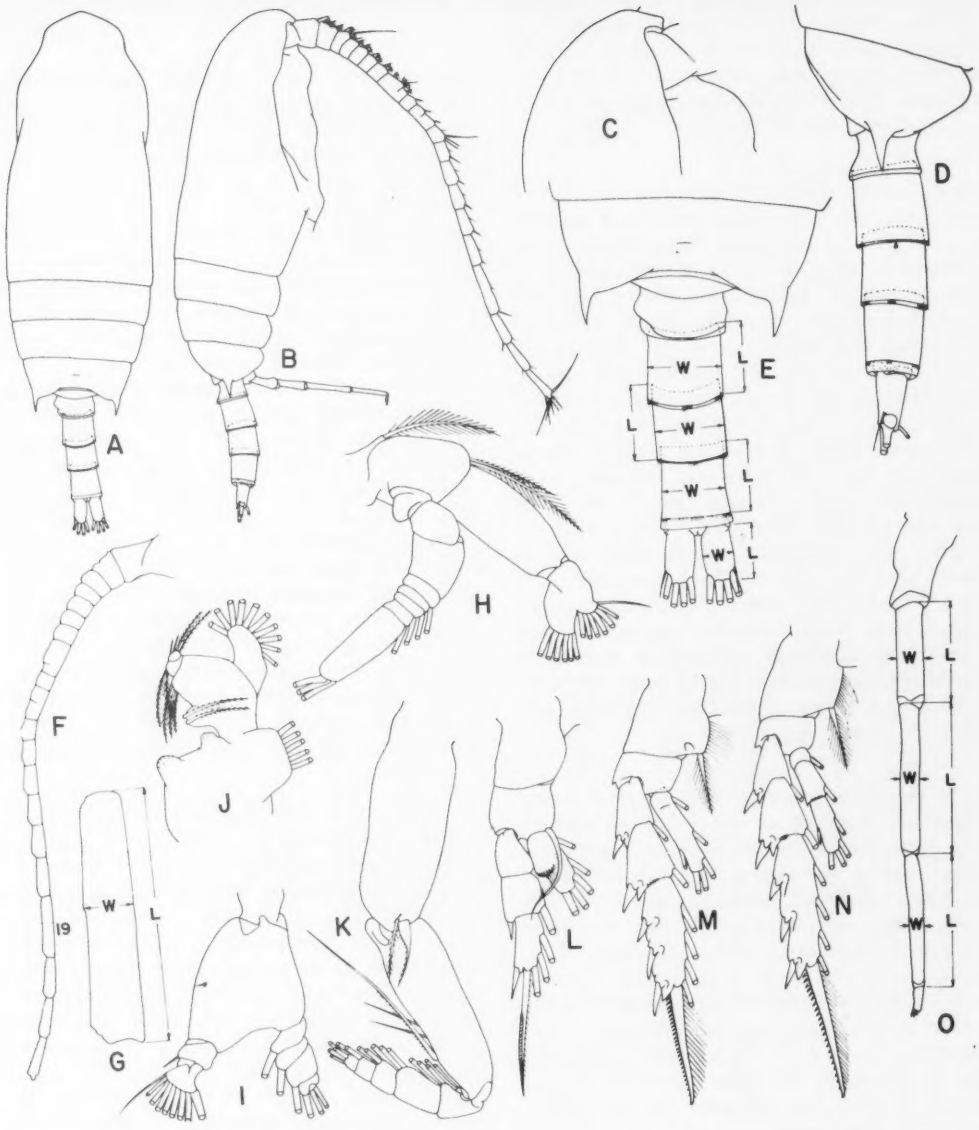

FIGURE 2.—*Actideus mexicanus*, new species. Male: A, habitus, dorsal; B, habitus, lateral; C, forehead, lateral; D, posterior part of body, lateral; E, posterior part of body, dorsal; F, antennule, setae omitted; G, 19th segment of antennule; H, antenna; I, mandible; J, maxillule; K, maxilliped; L, first leg, anterior; M, second leg, anterior; N, third leg, anterior; O, fifth leg, anterior. (L and W, length and width of segment.)

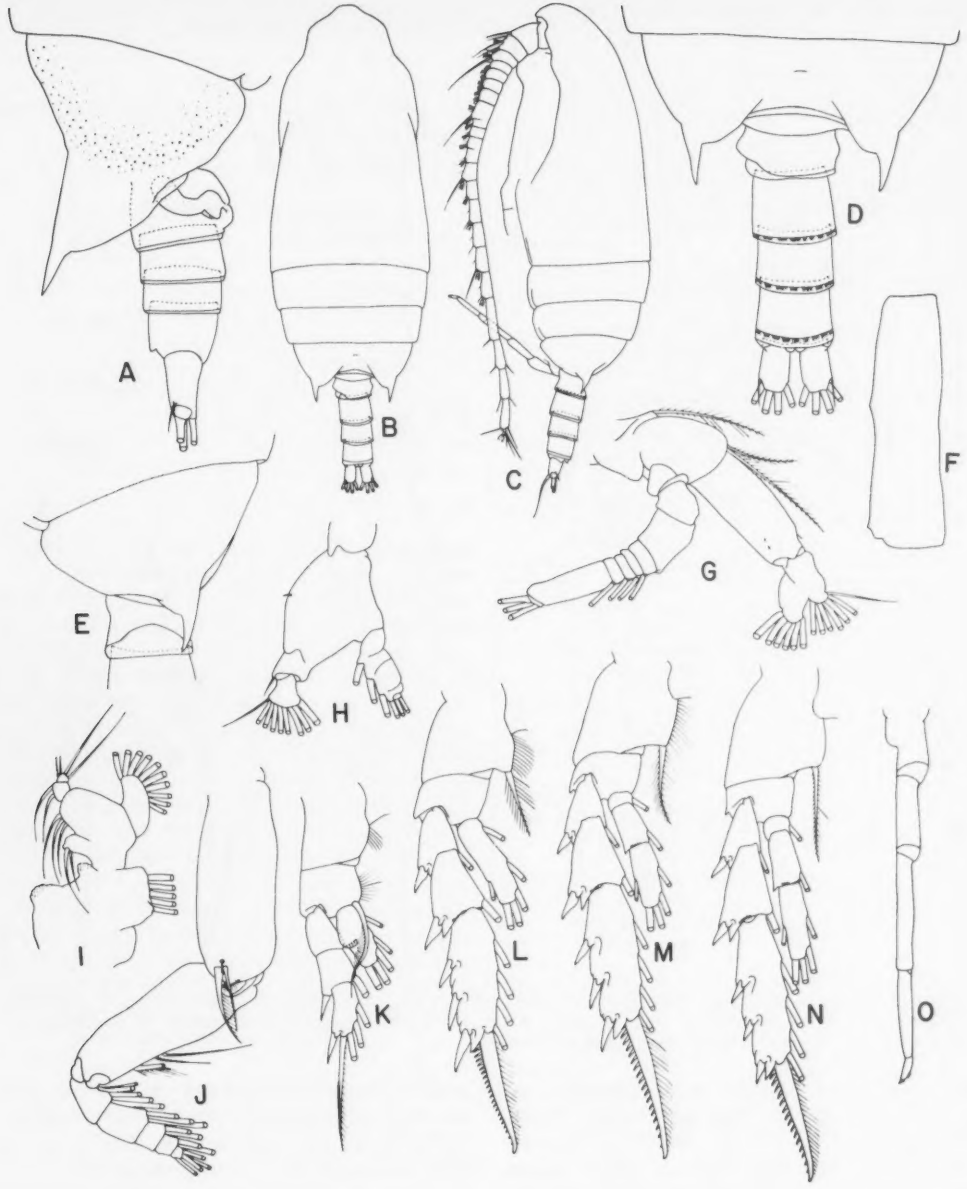

FIGURE 3.—*Aetideus acutus*. Female: A, posterior part of body, lateral. Male: B, habitus, dorsal; C, habitus, lateral; D, posterior part of body, dorsal; E, last metasomal and genital segments, lateral; F, 19th segment of antennule; G, antenna; H, mandible; I, maxillule; J, maxilliped; K, first leg, anterior; L, second leg, anterior; M, third leg, anterior; N, fourth leg, anterior; O, fifth leg, anterior.

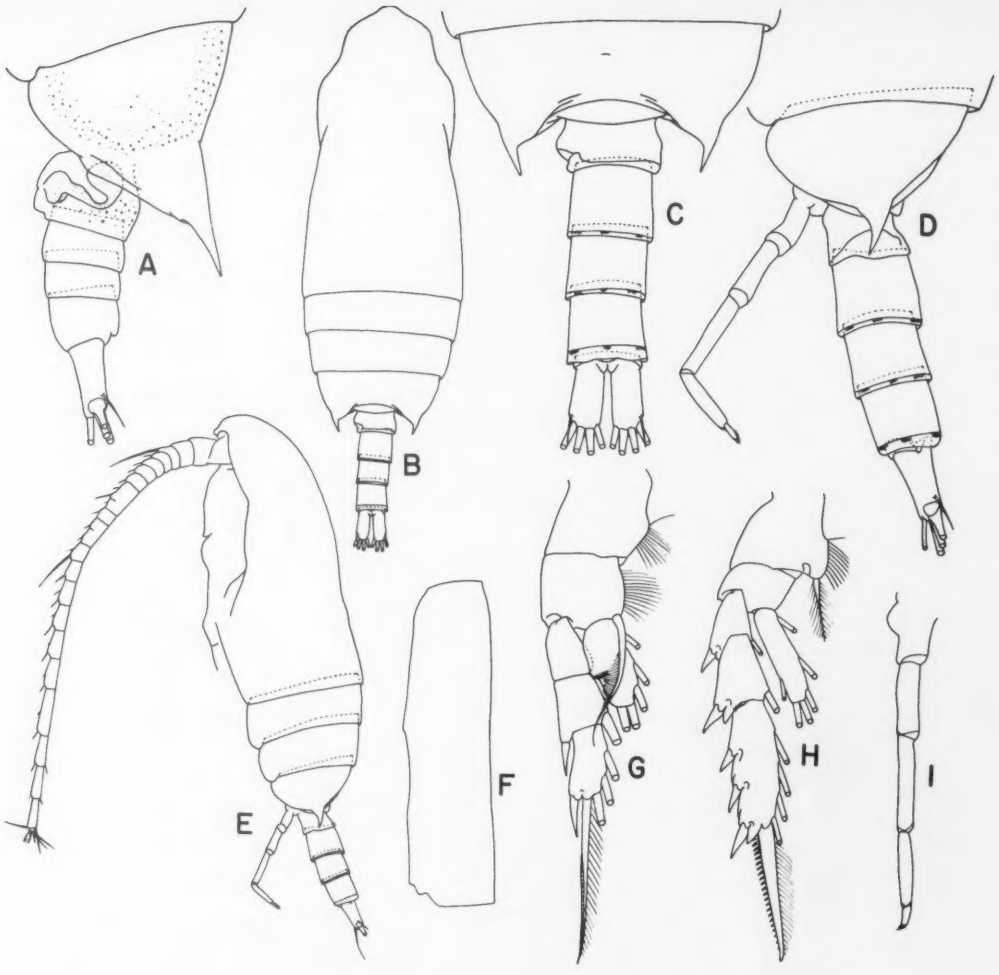

FIGURE 4.—*Actideus giesbrechti*. Female: A, posterior part of body, lateral. Male: B, habitus, dorsal; C, posterior part of body, dorsal; D, posterior part of body, lateral; E, habitus, lateral; F, 19th segment of antennule; G, first leg, anterior; H, second leg, anterior; I, fifth leg, anterior.

Distribution.—*A. acutus* was originally described from off New Zealand (Farran, 1929). The species has so far been known to occur on the Great Barrier Reef (Farran, 1936), in the Malay Archipelago (Vervoort, 1957), off the Pacific coast of Middle Japan (Tanaka, 1957; Tanaka and Omori, 1970), in the tropical Pacific (Grice, 1962), the northwestern Pacific (Brodsky, 1962), the central North Pacific (Park, 1968), the northeast Atlantic (Grice and Hulsemann, 1965), the Caribbean Sea and Gulf of Mexico (Park, 1970), and in the western Indian Ocean (De Decker and Mombeck, 1965; Grice and Hulsemann, 1967). In the Gulf of Mexico, *A. acutus* is the most common of all three *Aetideus* species so far known to occur, and it is mainly found in the upper 500 m.

AETIDEUS GIESBRECHTI CLEVE, 1904

Male.—Body length, 1.52-1.60 mm according to 50 randomly selected specimens. Propor-

tional lengths of prosome and urosome about 77:23. Dorsally, forehead (Figure 4B) produced as in *A. acutus*. Rostrum reduced. Metasomal process (Figures 4C, D) as in *A. acutus*. Second to fourth urosomal segments and caudal rami with width:length ratios of 1:0.93-0.95, 1:0.85-0.86, 1:0.88-0.89, and 1:2.27-2.38, respectively.

Antennules reaching about distal end of third urosomal segment, nineteenth and longest segment (Figure 4F) with width:length ratio of 1:3.75-3.86. Other cephalic appendages as in *A. acutus*. On second leg (Figure 4H), endopod extending beyond distal end of second exopodal segment. Terminal expodal spine longer than third exopodal segment, with about 24 teeth. Second to fourth segments of fifth leg (Figure 4I) with width:length ratios of 1:3.34-4.00, 1:6.00-6.25, and 1:5.00-6.65, respectively.

Remarks.—The male of *A. giesbrechti* is close to *A. mexicanus* in size but can be distinguished from it by the more produced forehead, wide and curved metasomal process, relatively short urosomal segments, wide nineteenth segment of the antennule, and long endopod of the second leg.

A. giesbrechti, including the male, was first described with figures by Giesbrecht (1892) under the name of *A. armatus*. Although the female has been reported by many authors, the male has since been found only by Bradford (1971). The female specimens found in the present study (1.84-2.08 mm in body length according to 76 randomly selected specimens) are in agreement with the descriptions given by Grice (1962) for the Pacific specimens. The appendages are identical with those of *A. acutus*, but the females of the two species are different in the form of spermatheca (Figure 4A).

Distribution.—As reviewed by Vervoort (1957), *A. giesbrechti* has been found throughout the world's oceans, except for the high latitudes. In the Gulf of Mexico the species is quite common in the upper 500 m.

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NORMAL POSTMORTEM CHANGES IN THE BROWN SHRIMP, *PENAEUS AZTECUS*[1]

DONALD V. LIGHTNER[2]

ABSTRACT

A study was carried out to determine the normal rates and patterns of gross and histologic postmortem changes in the brown shrimp (*Penaeus aztecus* Ives). Experimental shrimp were held at 10°, 20°, or 30°C in water-saturated air or in seawater at a salinity of 30‰. Observations were made at 0, 2, 4, 8, 12, 24, 48, and 72 h postmortem.

The first change observed grossly was the onset of a rigorlike stiffening of the abdominal musculature. This stiffening was noted at 2 h postmortem at 30°C, but disappeared by 12 h postmortem. The condition appeared later and persisted longer at the lower temperatures.

Histologically, the tubule epithelium of the hepatopancreas was the first tissue to show autolytic change. The autolysis in the remaining tissues examined occurred in the following order: foregut and midgut epithelium, heart, neurons and nerve fibers, antennal gland epithelium, gill epithelium, epidermis, muscle, and lastly connective and cuticular tissue elements. In all tissues the rate of autolysis was temperature-dependent.

Shrimp from the Gulf of Mexico represent one of the most valuable fishery products of the United States. Their popularity as a food item and for use as sportfishing bait in some coastal areas has resulted in recent studies aimed at developing methods of artificially culturing these animals. Despite the enormous value of shrimp as a seafood, little is known about their histology and the rates and patterns of postmortem change.

Postmortem biochemical changes in the muscle of brown shrimp (*Penaeus aztecus* Ives) were reported by Flick and Lovell (1972). They reported that the compounds ATP, ADP, AMP, IMP, and glycogen decreased with time postmortem, while inosine, hypoxanthene, and lactic acid increased. The latter compounds were suggested as being partly responsible for flavor deterioration of ice-stored shrimp. Tissue pH values increased from 7.4 to 8.2 after 10 days in ice-stored shrimp (0°C), and, according to these authors, even with advanced bacterial spoilage, increases in pH are usually observed in fish and shellfish. Shrimp tails remained tender and soft during the entire storage period of 10 days (at 0°C) and did not exhibit any of the characteristics commonly associated with rigor mortis (Flick and Lovell, 1972).

In the only histologic study of postmortem change in an invertebrate animal, Sparks and Pauley (1964) reported the normal postmortem changes in the oyster, *Crassostrea gigas*. The digestive tubules of the oyster underwent the most rapid autolytic change in dead oysters held at 14°-16°C, while the Leydig tissue, gut, stomach, mantle, gill and palps autolyzed somewhat less rapidly. The gonads were the most resistant of all oyster tissue to autolysis with ova and sperm appearing relatively normal even after all other tissues had undergone extensive autolysis.

There are certainly a number of factors which influence the rate of autolysis in a dead animal. Some of these factors include water temperature, dissolved oxygen concentration, pH, bacterial flora of the water and of the animal, and the physiological condition of the animal at the time of death. It has been demonstrated in man and other animals that postmortem changes occur in a regular and irreversible pattern and at a relatively constant rate from one individual to another when factors causing variation in the rate and pattern are considered (Sparks and Pauley, 1964). Differentiation of histological changes due to disease from those due to postmortem autolysis or poor fixation is possible once the normal rates and patterns

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of postmortem changes under various conditions are known.

The present study was undertaken to determine the normal rates and patterns of postmortem change in penaeid shrimp as an aid in distinguishing gross and histologic changes due to autolysis from changes due to disease.

MATERIALS AND METHODS

Juvenile brown shrimp averaging 50 mm in total length (tip of rostrum to tip of telson) were obtained live from a commercial bait dealer and were held in 500-liter fiberglass tanks for several days prior to being killed. Control shrimp were killed by immersion in fixative. The remaining shrimp were killed by placing the shrimp between wet towels in an enamel tray for 30 min. The shrimp were removed after 30 min and placed into 100-ml glass jars. Two groups at three temperatures (10°, 20°, and 30°C) were studied: one in air and the other in seawater. Shrimp held in air were introduced wet into test jars and the jars were sealed. Shrimp held in water were introduced into the test jars and enough Instant Ocean[3] artificial seawater (at 30 ‰ salinity) was added to fill the jars. Jars were held in wire baskets at midlevel in constant temperature baths.

Samples for antemortem examination were taken at 0 h while those for postmortem examination were taken at 2, 4, 8, 12, 24, 48, and 72 h. Four control shrimp were taken for study and two shrimp (one from seawater and one from air) were taken from the 10°, 20°, and 30°C baths at each of the remaining sampling times.

General appearance, color, odor, and condition of the hepatopancreas were noted at each sampling period. Tissues for microscopic examination were preserved in 10% buffered Formalin, prepared for microscopy with standard paraffin embedding and sectioning methods, and stained with hematoxylin and eosin.

RESULTS

Gross Observations

The first change observed was the onset of a rigorlike condition of the abdomen which appeared at about 2 h after death at 30°C and at 4 and 24 h at 20° and 10°C, respectively. The abdomen became flaccid at 12 and 48 h after death in shrimp held at 30° and 20°C, but at 10°C the abdomen remained rigid at 72 h after death (Table 1).

TABLE 1.—Time of onset of a rigor-like stiffening of shrimp abdominal musculature at 10°, 20°, and 30°C in air and seawater.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	−	−	−	−	−	−
2	−	−	+	−	+	+
4	−	−	+	−	+	+
8	−	−	+	+	+	+
12	−	+	−	+	−	−
24	+	+	+	+	−	−
48	+	+	−	−	−	−
72	+	+	−	−	−	−

+ = stiff
− = flaccid

Color change and the appearance of spoilage odor were first observed at 4 h after death at 30°C. The general appearance of the shrimp changed from the usual semitransparent to a whitish-opaque at about the same time the first trace of odor was detected (Tables 2 and 3). At 20° and 10°C the first color change and appearance of odor were noted at 12 h and 24 h, respectively. At all three temperatures the color of the shrimp changed from opaque to an orange-red and finally to red with some blackened areas (Table 2). The intensity of spoilage odor increased along with the color change (Tables 2 and 3).

Fluid leakage from the hepatopancreas was first observed at 4 h at 30°C and at about 8 and 12 h postmortem at 20° and 10°C. Enzymatic digestion of hepatopancreas and surrounding tissues was grossly evident at 12 h at 30°C as

TABLE 2.—Times of postmortem color change of whole shrimp at 10°, 20°, and 30°C in air and seawater.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	−	−	−	−	−	−
2	−	−	−	−	−	−
4	−	−	−	−	0	0
8	−	−	−	−	0	0
12	0	−	−	0	LR	LR
24	LR	0	LR	LR	Rb	Rb
48	LR	LR	R	Rb	Rb	R
72	Rb	R	Rb	R	Rb	Rb

− = normal
0 = opaque
LR = orange to light red
R = red
Rb = red with blackened edges of cuticle or blackened appendages

[3] Reference to trade names in this publication does not imply endorsement of commercial product.

TABLE 3.—Time of appearance of postmortem spoilage odor in whole shrimp held at 10°, 20°, and 30°C in air and seawater.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	–	–	–	–	–	–
2	–	–	–	–	–	–
4	–	–	+	–	+	+
8	–	–	++	–	+	+
12	–	–	++	–	++	++
24	+	+	++	++	++	++
48	++	+	+++	+++	+++	+++
72	++	++	+++	+++	+++	+++

– = normal
+ = odor

indicated by a loosening of the junction of the cephalothorax and abdomen. By 48 h the junction was very loose and by 72 h the tissues of the junction appeared mostly liquified. At 10° and 20°C the same process was observed but at a proportionately slower rate.

Histological Observations

Since the same patterns of autolysis were seen in shrimp held at all three temperatures, the differences being a function of time (Table 4), only the histological results from the 30°C portion will be presented in the text. The only significant histological differences between groups held in air and water noted were the more rapid tissue decomposition due to increased bacterial action in animals held submerged in seawater.

Digestive Tract

According to Roberts (1966), the digestive tract in shrimp is composed of three divisions: (1) the foregut, which includes the mouth, esophagus, stomach, and associated glands; (2) the midgut and hepatopancreas; and (3) the hindgut. Of these organs the hepatopancreas, the foregut, and midgut were studied in detail. The hindgut was not studied.

Hepatopancreas

The glandular hepatopancreas is the first organ to undergo autolytic change (Figure 1a). This organ is a compound tubularacinar exocrine gland composed of tubules which end in blind sacs or acini. The tubules and acini are lined with a simple low to high columnar epithelium (Figure 1b). Autolysis of the epithelium of this

TABLE 4.—Rate of postmortem histologic change in shrimp held in air or seawater at three temperatures.

a. Hepatopancreas.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
2	2.5*	2.5	2.5	2.5	3	3.5
4	4	4	4	4	4	4
8	4	3.5	4.5	5	4.5	4.5
12	3.5	4	—	—	5	5
24	5	4	5	5	5	5
48	5	5	5	5	5	5
72	5	5	5	5	5	5

b. Midgut epithelium.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
2	1*	1	1	1	1-2	1
4	2	1	1-2	1-2	—	2
8	4	—	4-5	—	3	4
12	—	3	2	4	5	4
24	5	4	—	5	5	—
48	5	5	5	5	—	5
72	5	5	5	5	5	5

c. Abdominal muscle.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
2	0	0	0	0	0	0
4	1	1	2	1	1.5	1
8	0	1	2	2	2	2
12	1	1	2.5	2.5	3	3
24	3	3	3.5	3	3.5	3.5
48	2.5	3	4	4	3.5	4.5
72	4	3.5	4.5	4	4.5	4

d. Epidermis.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
1	0	0	0	0	0	0
2	0	0	0	0	0	0
4	0	1	—	—	2	2
8	1	1	—	2	3	3
12	2	2	3	3	4	4
24	3	3	3	3	4	—
48	3	3	4	4	5	5
72	5	5	5	5	5	5

— No observation made.
* Average assigned values from a scale of 0 to 5 denoting the general histological appearance of the tissue or organ.
0 = Normal histologic appearance, like the control, no postmortem change.
1 = Slight change, scattered pyknotic nuclei, slight staining differences.
2 = More advanced cellular change with increases in nuclear pyknosis, karyrhexis, karyolysis, some cytolysis; loss of normal appearance or structure of the tissue or organ.
3 = Further advanced change with no normal appearing areas.
4 = Advanced autolytic change, tissue or organ represented by cellular debris or by its fibrous or cuticular stroma.
5 = Complete autolysis, tissue or organ no longer demonstrable.

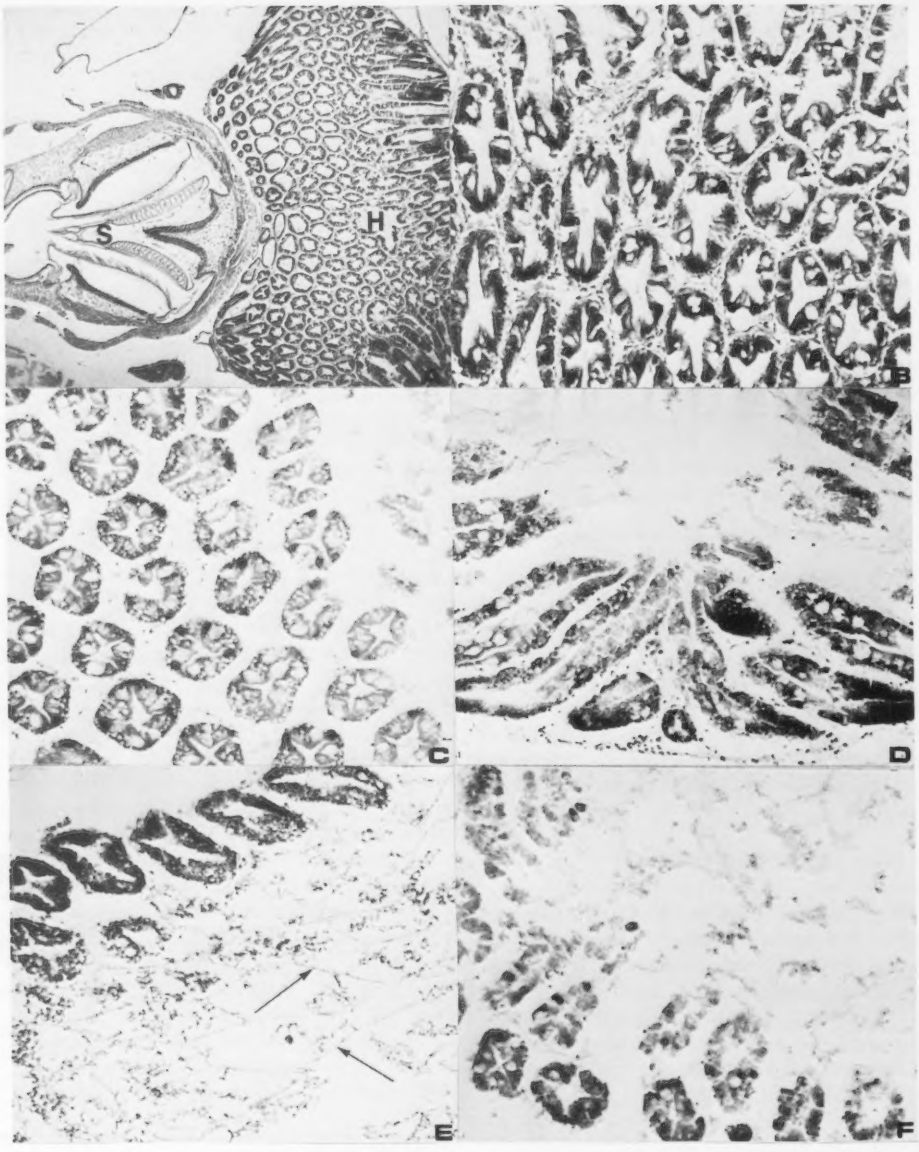

FIGURE 1.—**a.** Normal stomach (S) and hepatopancreas (H). 25×. **b.** Normal hepatopancreas. 120×. **c.** Hepatopancreas at 2 h postmortem showing edematous swelling between adjacent tubules. Autolysis is more advanced nearer the center of the organ (upper right) than at the periphery (left). 110×. **d.** Hepatopancreas at 4 h postmortem showing tubules on longitudinal section. Note the progression of autolytic change in the tubules from the periphery of the organ (bottom) to the autolyzed center (top). 110×. **e.** Hepatopancreas showing near complete autolysis (4 h postmortem). Note network of connective tissue stroma (arrows) remaining after autolysis of tubule epithelium. 120×. **f.** Hepatopancreas at 8 h postmortem showing advanced autolysis. Intensely pyknotic nuclei are present in the remaining epithelial cells near the periphery of the organ. Tissue debris and remnants of the connective tissue stroma are present nearer the organ's center (upper right). 120×.

organ proceeds so rapidly that by 2 to 4 h postmortem, the epithelium of tubules near the center of the organ showed advanced autolysis. These tubules showed desquamation and cytolysis of the lining epithelium and replacement with eosinophilic debris (Figures 1c and 1d). Nearer the periphery of the organ, the condition of the tubules and tubule epithelium appeared progressively more normal, with the most normal appearing tubules and acini at the periphery (Figures 1c and 1d). In the band of tissues between the normal appearing periphery and the lysed core, all stages of cell death were observed. A thin band of tissue in this area contained tubules whose epithelial cells possessed scattered pyknotic nuclei and had slight cytoplasmic staining differences (Figure 1e). Deeper to this layer the epithelial cells of tubules and acini possessed scattered pyknotic nuclei and had slight cytoplasmic staining differences (Figure 1e). The cytoplasm of these cells was highly vacuolated and stained variably with hematoxylin and eosin but generally much less basophilicily than normal (Figure 1c). At this time the spaces between adjacent tubules and acini had become swollen (Figures 1c and 1d). Slightly deeper to this layer epithelial cell nuclei had undergone karyorrhexis or karyolysis and disappeared. Many of the cells of this area had lysed and the cellular debris stained red with eosin. The supportive stroma of the hepatopancreatic tubules remained intact in some areas after the epithelium had autolyzed, thereby masking the former site of the hepatopancreatic tubules (Figure 1e).

By 8-12 h postmortem even the tubules and acini at the periphery of the organ showed advanced autolytic change, and the tissue debris and remnants of supportive stroma in the center of the organ were liquified (Figure 1f). The connective tissue capsule of the organ had become ruptured and few recognizable tubules were present. Past 12 h no trace of the hepatopancreas was present, and surrounding tissues had also been partially or completely digested, presumably by enzymes released from the autolyzed hepatopancreas.

Foregut and Midgut

Autolytic changes in the foregut, particularly the epithelium of the stomach (Figure 1a), proceeded at approximately the same rate as changes in the hepatopancreas. Nuclear changes within epithelial cells were observed at 2 h postmortem with considerable change by 4 h. By 8 to 12 h the epithelium of the stomach had undergone nearly complete autolysis and had disappeared, leaving only the cuticular elements of the stomach lining intact. The cuticular elements of the esophagus and stomach persisted for the duration of the study (72 h).

The midgut extends from the pyloric stomach to the sixth abdominal segment where it joins with the hindgut (Roberts, 1966). It is without a lining cuticle. The first autolytic change in the midgut was observed in the lining epithelium at 2 to 4 h, when the epithelial cells began to show changes such as scattered pyknotic nuclei, changes in staining reaction from a pale basophilic reaction to a more eosinophilic one, and the "blebing" of the apical ends of epithelial cells into the gut lumen (Figure 2a). The epithelium usually remained attached to the basement membrane at 2 h, but in some areas portions of the midgut epithelium had been sloughed into the gut lumen (Figures 2b and 2c). Sloughed epithelial cells were rounded and had intensely pyknotic nuclei and a uniform eosinophilic cytoplasm. At this time the gut lumen usually contained a fibrous, eosinophilic coagulum (Figure 2b). The gut wall basal to the lining epithelium showed no appreciable changes by 4 h.

By 8 to 12 h the midgut epithelium had been sloughed into the gut lumen (Figure 2d). The epithelial cells in the gut lumen were rounded, and some had pyknotic nuclei, but they were mostly anucleate. Many of the epithelial cells had lysed and left behind amorphous masses of eosinophilic debris (Figure 2d). Changes in the cellular elements of the wall of the midgut became apparent by 8-12 h. These changes consisted primarily of a decrease in nuclear number in the muscle and connective tissue cells present and pyknosis of those nuclei remaining (Figure 2d). In general, the cytoplasm of the cells present showed increased eosinophilia.

No trace of the lining epithelium was present after 24 h (Figure 2e). The coagulum, which was present in the gut lumen of some animals at 2-8 h, was still present. Also present in the gut lumen were large numbers of bacteria (Figure 2e). No nuclei were present in the gut wall, and the cellular elements remaining stained intensely with eosin.

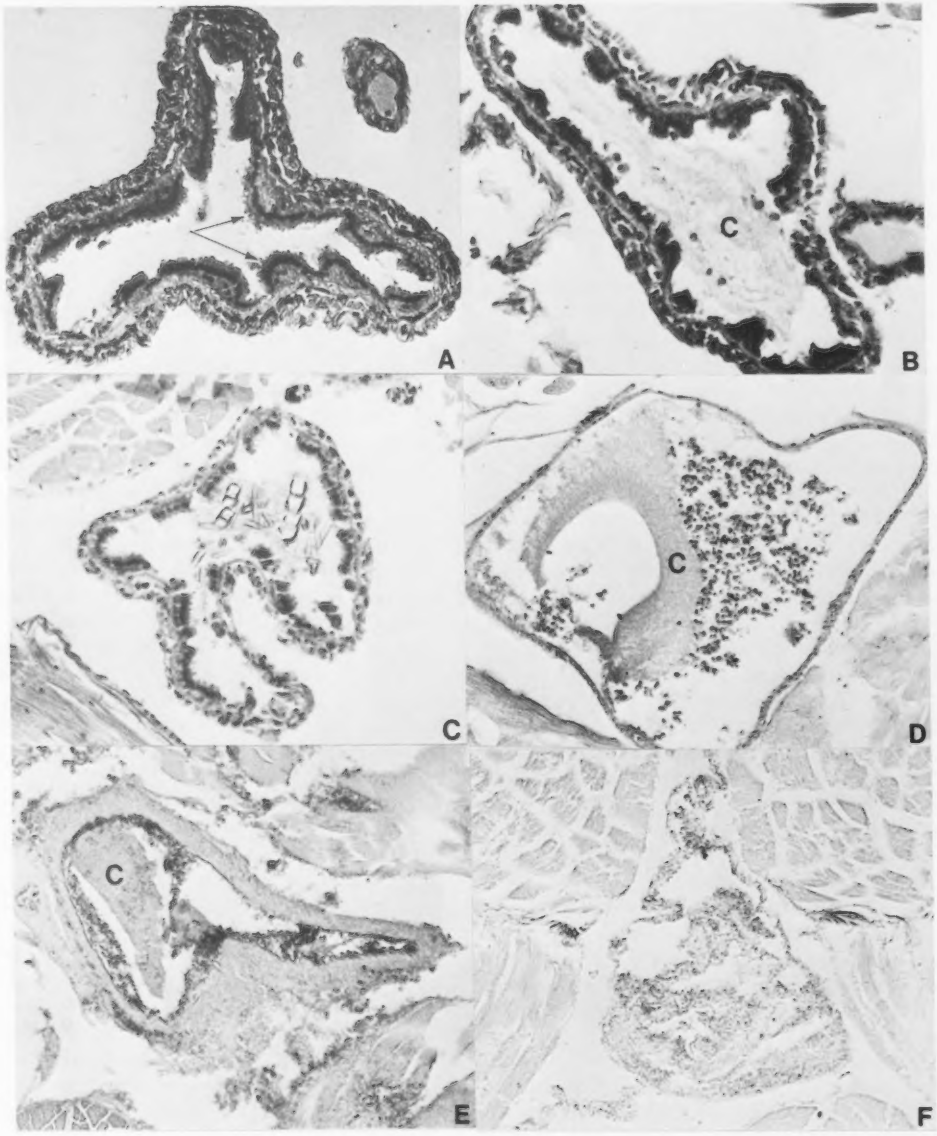

FIGURE 2.—**a.** Cross section of midgut at 2 h postmortem. The appearance is near normal except for the "blebing" of the apical ends of some of the epithelial cells (arrows) and a few pyknotic nuclei. 250×. **b.** Midgut showing more advanced autolytic change at 2 h postmortem. Some epithelial cells have been sloughed into the gut lumen where an eosinophilic coagulum (C) has formed. 240×. **c.** Midgut at 4 h postmortem. Most of the epithelial cells possess pyknotic nuclei, and some of the cells have been sloughed into the gut lumen. 210×. **d.** Midgut at 8 h postmortem. Sloughed epithelial cells are rounded and are either anucleate or have pyknotic nuclei. An eosinophilic coagulum is present. 160×. **e.** Midgut at 24 h postmortem. An eosinophilic coagulum is present in the gut lumen as are numerous bacteria. No trace of the gut epithelium remains. The muscle and fibrocyte cells of the gut wall are anucleate. 190×. **f.** Site of midgut at 48 h postmortem. Bacteria and debris have filled the gut lumen. Only fibrous elements of the gut wall remain. 150×.

By 48 h, the gut wall had become thin and was frequently interrupted. The gut lumen was filled with bacteria and other debris (Figure 2f). By 72 h, all traces of the gut, including the gut wall, had disappeared leaving the former site of the gut marked only by masses of bacteria and amorphous eosinophilic cellular debris.

Heart and Major Vessels

In shrimp the heart lies immediately dorsal and slightly caudad to the large hepatopancreas. Only the thin connective tissue coverings of the two organs separate them. Hence, autolysis of the hepatopancreas and release of its proteolytic enzymes results in a rapid destruction of the rather loose tissues of the shrimp heart (Figure 3a). The hepatopancreas showed considerable autolytic change by 4 h postmortem leaving the heart barely recognizable (Figure 3b). By 8 h the heart was not distinguishable from the other tissue debris present at the heart's former location in the cephalothorax. Vessels in the vicinity of the hepatopancreas and heart also disappeared by 4-8 h, but vessels elsewhere, such as in the abdomen, persisted much longer, some still recognizable after 24 h. However, by 48 h vessels were not usually demonstrable anywhere in the body of a shrimp.

Musculature

Shrimp locomotory muscle is striated and presents a histologic appearance that is similar to that of vertebrate striated muscle (Figure 4a). The muscles of the cephalothorax in the vicinity of the hepatopancreas underwent rapid autolytic change, apparently due to digestion by enzymes released on lysis of the hepatopancreas. Further from the hepatopancreas, the rate of autolytic change in the muscle was much slower. The earliest observed postmortem change in the muscle was at 4 h when some individual muscle fibers had a slightly "frayed" appearance. There was a pronounced swelling, presumably edematous, between adjacent muscle fibers (Figure 4b). By 8-12 h, muscle cell nuclei had become pyknotic. After 24 h muscle cells had become anucleate, highly eosinophilic, and the edematous swelling between adjacent muscle cells had decreased. Cross striations within muscle fibers were especially evident (Figures 4d, 4e, and 4f).

In some, but not all, of the shrimp studied, bacterial growth was evident between muscle bundles, especially in the vicinity of the gut. The presence of large numbers of bacteria greatly increased the rate of tissue deterioration (Figure 4c), while muscle not heavily invaded by bacteria remained recognizable as muscle tissue at 72 h (Figure 4f).

Integument

The integument, consisting of epidermis and an overlying cuticle, underwent rapid degeneration in the area of the cephalothorax that surrounds the hepatopancreas, leaving only

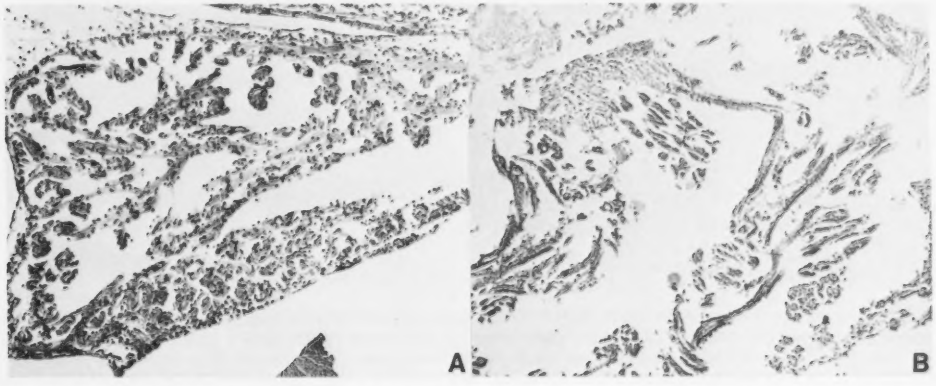

FIGURE 3.—**a.** Normal heart. 110×. **b.** Heart at 4 h postmortem showing considerable autolytic change and loss of structural detail. 100×.

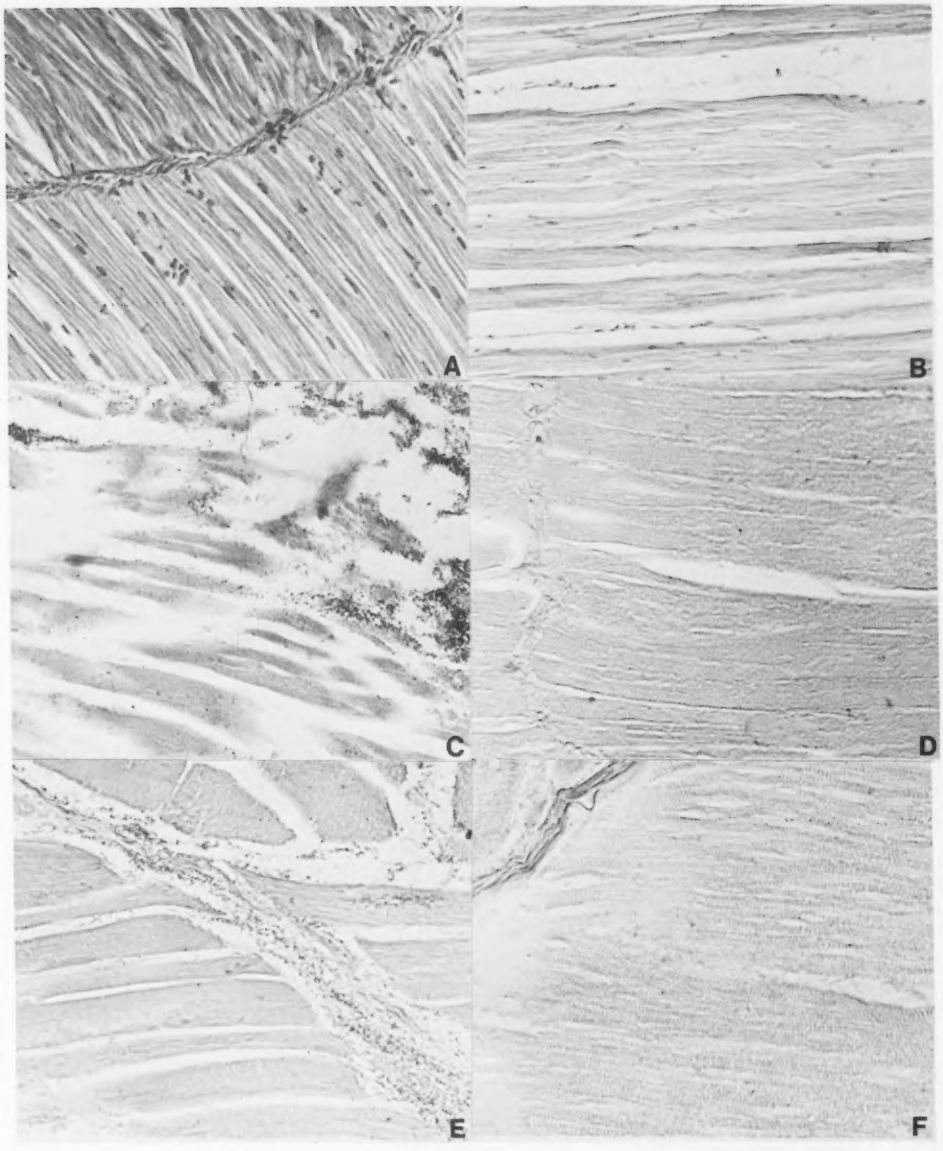

FIGURE 4.—**a.** Normal abdominal muscle. 220×. **b.** Muscle at 4 h postmortem showing edematous swelling between muscle bers. Sarcoplasmic staining reaction is more eosinophilic than normal and there has been a decrease in the number of nuclei although few pyknotic nuclei are shown. 150×. **c.** Muscle showing advanced autolytic change due to the presence of large amounts of bacteria (12 h postmortem). 190×. **d.** Muscle at 24 h postmortem. Edematous swelling has decreased, but the muscle fibers have become anucleate. Note the prominence of cross striations. 240×. **e.** Muscle at 48 h postmortem. 240×. **f.** Muscle fibers with prominent cross striations are still recognizable at 72 h postmortem. 250×.

the cuticle remaining by 4 h. Distant from the hepatopancreas, the epidermis showed pyknotic nuclei and cell rounding by 4 to 8 h (Figures 5a and 5b). A slight hemocytic response was present at this time in the subepidermal tissue layers representing the only inflammatory-like response observed in the study.

The epidermis had frequently become detached from the overlying cuticle by 12 to 24 h postmortem and many of the epidermal cells had lysed, with those remaining having pyknotic nuclei (Figure 5c). By 24 to 48 h nearly all traces of the epidermis had been lost and in some animals examined only cellular debris or clumps of bacteria marked its former location (Figure 5d). Though usually interrupted, the cuticle was the most resistant structure to autolytic change and showed only slight histological change by 72 h.

Gills

The shrimp respiratory system consists of paired gills in the branchial chambers of the cephalothorax. The structure of the gills is dendrobranchiate (Barnes, 1963). The gills are covered by a thin cuticle underlain by a thin epithelium and other supportive cells (Figure 6a).

A peritrichous ciliated protozoan (Figure 6b), presumably a commensal on shrimp (especially common on the gills but also found elsewhere on

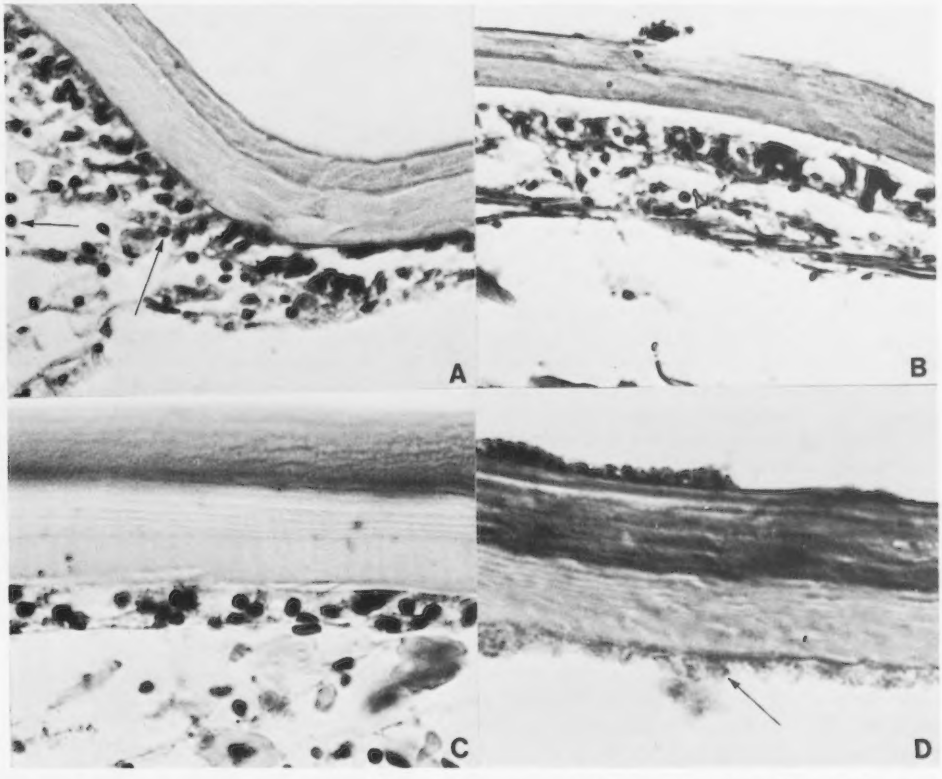

FIGURE 5.—**a.** Integument consisting of epidermis and overlying cuticle at 4 h postmortem. Some of the epidermal cells possess pyknotic nuclei. A few hemocytes are present in the subepidermal tissues (arrows). 480×. **b.** Integument at 8 h postmortem. Inflammatory cells are present in the subepidermal tissue. There is an increase in nuclear pyknosis in the epidermis and in the subepidermal tissue. 300×. **c.** Epidermis and cuticle at 24 h postmortem. All of the epidermal cells have intensely pyknotic nuclei, as does all the subepithelial tissue. 600×. **d.** Integument at 48 h postmortem. The cuticle is present, but the epidermis is represented by debris (arrows). 750×.

the body surface), increased rapidly in numbers for 2 to 4 h after death of the shrimp. They were absent by 8 h postmortem.

The cellular elements of the gills underwent fairly rapid autolytic change. By 8-12 h scattered pyknotic nuclei were present (Figure 6c). By 24 h the cellular elements of the gills were for the most part anucleate, with some portions of the gills having only eosinophilic debris within the lamellar cuticle (Figure 6d). By 48 h the thin cuticle of gill lamellae had begun to deteriorate and hence the gill lamellae sectioned transversely began to lose their typical "dumbbell" appearance (Figure 6e). By 72 h the gills were usually no longer demonstrable histologically, but in one of four animals examined portions of the gills were still evident (Figure 6f).

Nerve Tissue

The nervous system of shrimp is composed of a large ventral nerve cord and segmental ganglia from which smaller nerve branches originate to innervate the tissues. At the anterior end of the ventral nerve tract is the supraesophageal ganglion, which anteriorly receives the large optic nerve tracts.

Neuron perikaryons in the ganglia (Figure 7a) underwent the most rapid autolytic change of the various elements of shrimp nerve tissue. After 2 to 4 h, these cells showed considerable rounding, pyknotic or karyolytic nuclei, and a change in cytoplasmic staining from highly basophilic to a lesser basophilic to almost eosinophilic (Figure 7b). By 8 h no trace of neuron perikaryons was evident.

The nerve tracts of the ventral nerve, its branches, and the optic nerves autolyzed less rapidly than did neuronal perikaryons. However, nerve cell processes (axons and dendrites) within the nerve tract autolyzed more rapidly than did the supportive neurolemmal and glial cells, and were no longer demonstrable histologically by 12 to 24 h (Figure 7c). The supportive glial cells of the nerve tracts persisted without noticeable change to 8 to 12 h, but these cells became anucleate or underwent autolysis after 24 h, and their former presence was represented only by debris and an occasional pyknotic nucleus (Figure 7d).

After 24 h postmortem, the basic structural arrangement of the nerve tract remained recognizable due to the persistence of neurolemmal fibers (Figures 7d and 7e), which persisted to 72 h at the sites of the optic nerve and ventral nerve tracts.

Antennal Gland

The antennal gland of crustaceans had been demonstrated to be important in ion regulation (Robertson, 1959). The antennal or hemocoelic excretory gland in shrimp is located in the cephalothorax above the supraesophageal ganglion (Young, 1959). The gland is composed of a collection of tubules and a bladder (Figures 8a and 8b). By 4 h some sloughing of tubule epithelium was evident (Figure 8b), but for the most part the histologic appearance of the organ remained normal. At 12 h, however, most of the nuclei of the tubule epithelium were intensely pyknotic (Figure 8c), and by 24 h the organ had disappeared or had become difficult to recognize (Figure 8d). No trace of the gland was found after 48 h postmortem.

Gonadal Tissue

Since the animals used in this study were immature juvenile shrimp, the gonads were small, poorly differentiated and were located in the cephalothorax lateral and slightly caudad to the hepatopancreas. The terminal ampule of male shrimp was poorly developed and in female shrimp the ovarian lobe, which extends into the abdomen in older shrimp, had not yet developed.

The rate of autolysis in the gonads of the shrimp studied was rapid, due to their close proximity to the hepatopancreas. Gonadal tissue was not recognizable histologically after 4 to 8 h postmortem.

DISCUSSION

The rigorlike stiffening observed in this study may represent true rigor mortis. Sparks (1972) postulated that rigor mortis or a similar phenomenon may occur in some invertebrates with well organized skeletal systems and associated skeletal muscles. He based his opinion on the observation that many arthropods, which are flaccid after somatic death, subsequently

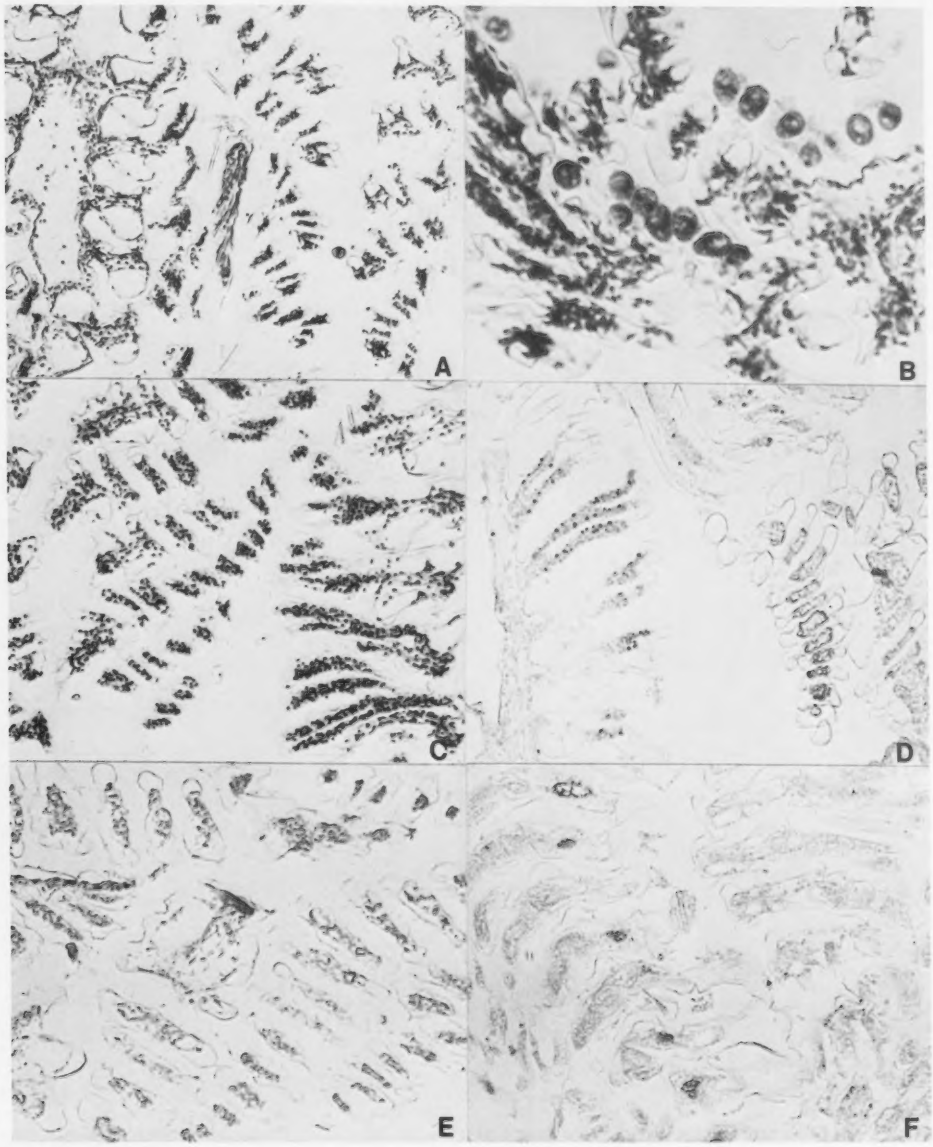

FIGURE 6.—**a.** Normal gills. 120×. **b.** An unidentified ciliated protozoan abundant on the gills at 4 h postmortem. 240×. **c.** Gills at 12 h postmortem. Note the absence of the protozoan and the presence of pyknotic nuclei in the cellular elements. 130×. **d.** Gills at 24 h postmortem. Except for a few pyknotic nuclei only the cuticle and cellular debris remain. 160×. **e.** Gills at 48 h postmortem. The tissue is still recognizable as gills; however, the lamellae are losing their usual "dumbbell" appearance and contain only eosinophilic cellular debris. 190×. **f.** Gills at 72 h postmortem. Gills were recognizable histologically only from this one of four animals examined. 120×.

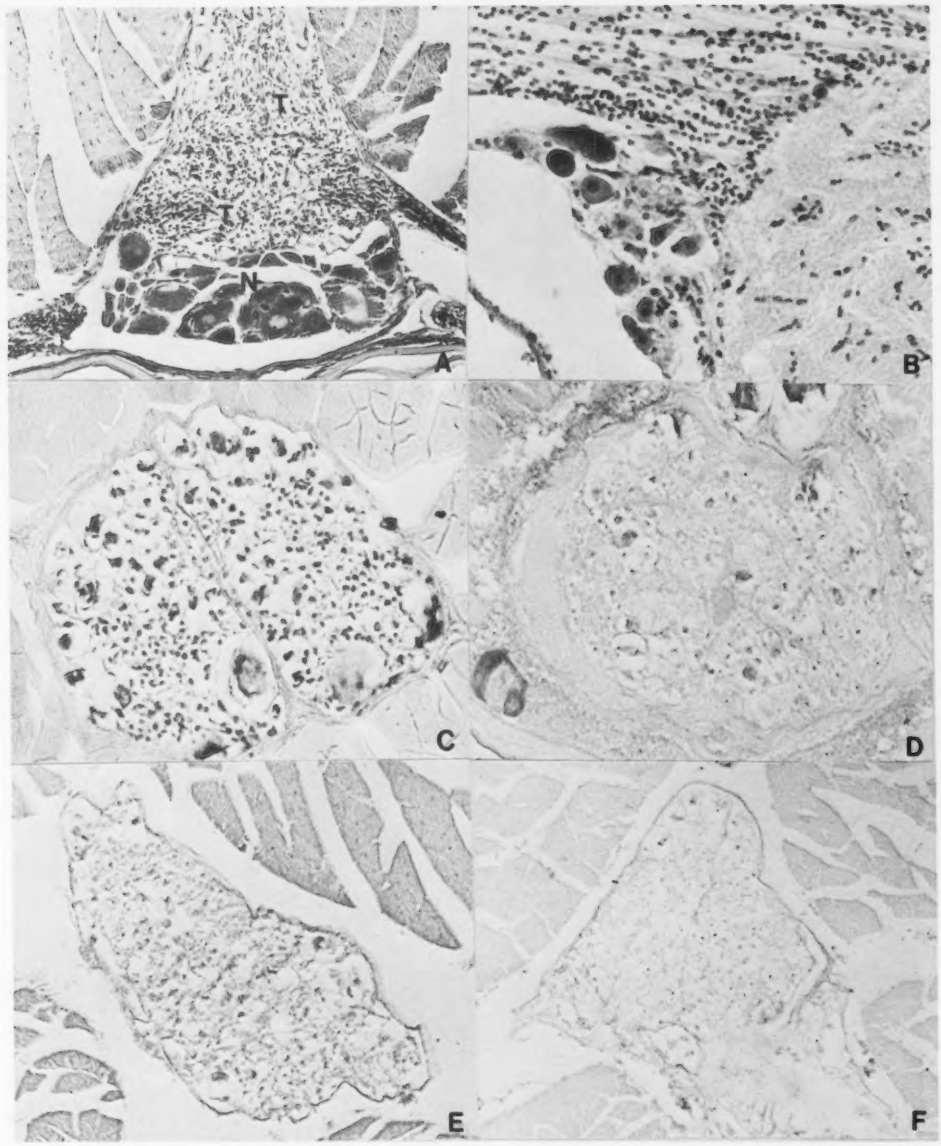

FIGURE 7.—**a.** Cross section of an abdominal segment ganglion on the ventral nerve (0 h control). Neuron perikaryons (N) are present ventral to the large ventral nerve tract (T). 110×. **b.** Sagittal section of an abdominal segment ganglion at 4 h postmortem. The neuron perikaryons are rounded and have pyknotic nuclei. Nerve cell processes, neurolemmal and glial cells in the nerve tract show no apparent autolysis. 220×. **c.** Cross section of the ventral nerve at 12 h postmortem. Nerve cell processes are not evident and neurolemmal and glial cells possess pyknotic nuclei. 200×. **d.** Cross section of the ventral nerve at 24 h postmortem. Only supportive fibrous tissue elements and eosinophilic debris remain. 190×. **e.** Cross section of ventral nerve at 48 h postmortem. Fibrous elements are still present. 200×. **f.** Ventral nerve in cross section at 72 h postmortem. The fibrous elements of the nerve are still present. 120×.

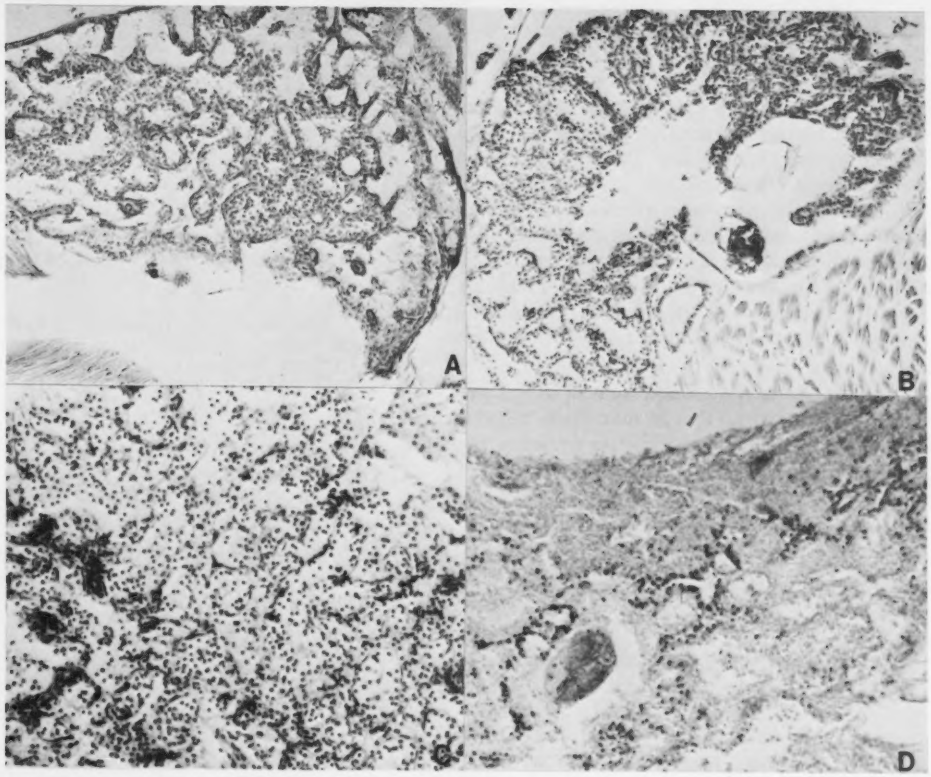

FIGURE 8.—**a.** Normal antennal gland. 100×. **b.** Antennal gland at 4 h postmortem. A few epithelial cells have been sloughed into the tubule lumens. 100×. **c.** The tubule epithelium of the antennal gland at 12 h postmortem showing intense nuclear pyknosis. 150×. **d.** Antennal gland at 24 h postmortem. The tubule epithelium has lysed filling the tubule lumens with eosinophilic debris and nuclear remnants. 150×.

become rigid. Whether this was due to desiccation of the tissues or actual rigor of the muscles was not determined. In the present study, freshly killed juvenile shrimp became rigid in sealed glass jars containing water-saturated air and when totally submerged in water. Desiccation was not possible. The time of onset of rigidity was, as in vertebrates, temperature-dependent, occurring earlier at higher temperatures than at lower temperatures.

Flick and Lovell (1972) in studying postmortem biochemical changes in penaeid shrimp reported that shrimp tails remained soft and did not exhibit any of the characteristics commonly associated with rigor mortis during a storage period of 10 days at 0°C. Perhaps the effect of freezing or near-freezing temperature on shrimp muscle either masks or inhibits the onset of physical rigor.

The rate of autolysis of the hepatopancreas is extremely rapid. The organ is a large, multifunctional organ believed to produce the bulk of enzymes used in the digestive process in shrimp and to have some absorptive and storage function. The hepatopancreas connects to the midgut near its origin from the pyloric stomach. The gut is a short, nearly straight tube, and, hence, enzymatic digestion must occur as rapidly as possible if the shrimp is to utilize its food efficiently. Even careful handling of shrimp to avoid stress before fixation, opening of the cuticle over the hepatopancreas, or excision and bisection of the gland to enhance fixation, frequently failed to provide adequate penetration and fixation of the organ when Formalin fixatives were used. The remaining tissues of shrimp are generally adequately fixed for light microscopy with Formalin, provided

that small pieces of tissue are used or that the cuticle is opened on smaller shrimp that are fixed whole.

The relative rates and patterns of postmortem change in shrimp are similar to those described for the oyster (Sparks and Pauley, 1964) and for mammals (Cruickshank, 1912; Smith and Jones, 1966). In mammals, oysters, and shrimp, tissues that produce large amounts of proteolytic enzymes such as the mammalian pancreas and lining epithelium of the stomach, oyster digestive tubules, and shrimp hepatopancreas and gut epithelium autolyze the most rapidly. Tissues that autolyze nearly as rapidly are high lipid containing tissues such as nerve tissue. In the shrimp and in mammals, muscle, connective, and epidermal tissues undergo the least rapid autolysis.

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BOTHUS THOMPSONI (FOWLER) 1923, A VALID SPECIES OF FLATFISH (PISCES:BOTHIDAE) FROM THE HAWAIIAN ISLANDS

PAUL STRUHSAKER AND ROBERT M. MONCRIEF[1]

ABSTRACT

Bothus thompsoni (Fowler) 1923 is resurrected from the synonymy of *B. bleekeri* Steindachner and redescribed. *B. thompsoni* differs from all other recognized species of the genus in possessing 11-17 gill rakers on the lower limb of the first gill arch and 115-147 lateral line scales. *B. thompsoni* is endemic to the Hawaiian Islands where it inhabits the outer shelf in depths of 70-115 m.

Fowler (1923) proposed *Platophrys thompsoni* on the basis of a single specimen obtained by John W. Thompson. Although no exact locality data were given, we assume the specimen was from the Honolulu market. *Platophrys* is now considered a synonym of *Bothus*, while Norman (1934), without comment, relegated *Bothus thompsoni* to the synonymy of *B. bleekeri* Steindachner. Gosline and Brock (1960) followed Norman in listing *B. bleekeri* from the Hawaiian Islands. Previously, only the holotype of *B. thompsoni* was available for study. Our examination of numerous specimens collected by the National Marine Fisheries Service (NMFS) during recent bottom trawling surveys in the 60-700 m depth range of the Hawaiian Islands demonstrates that *B. thompsoni* should be recognized as a valid species.

MATERIAL AND METHODS

All specimens were collected with 12.5-m (headrope) shrimp trawls during bottom trawling surveys in the Hawaiian Islands with the NMFS RV *Townsend Cromwell*. Sampling effort and general ichthyological results of these surveys are given by Struhsaker (1973). Most specimens examined (one exception from Maui) were from the north coast of the island of Oahu.

The following description is based on a series of 29 male (55.8-114.4 mm SL) and 31 female (39.1-103.7 mm SL) specimens all of which are housed in the National Museum of Natural History (USNM) and Bernice P. Bishop Museum (BPBM). Additionally, 33 uncatalogued specimens cleared and stained by the method described by Taylor (1967) were utilized in vertebral and gill raker counts, and more uncatalogued specimens were examined, obtaining supplementary dorsal, anal, and caudal ray counts.

Measurements and counts are usually as defined by Norman (1934), Hubbs and Lagler (1958), and Gutherz (1967). Standard length was taken from tip of snout to end of hypural plate on the blind side. Horizontal eye diameter was taken between edges of the bony orbits. Snout to axis of greatest depth was taken from the snout to a vertical line at the greatest body depth. The last two dorsal and anal rays are each associated with pterygiophores and are counted as two. Lateral line scale rows just above the lateral line and pored lateral line scales were counted. Vertebral counts were taken from radiographs and from cleared and stained specimens. Gill rakers were counted as discussed below.

To evaluate morphometric characters, measurements in original units and as percent of standard length were plotted as functions of standard lengths.

RESULTS

Description

Although a figure of *B. thompsoni* did not accompany the original description, Fowler (1928), in listing the species for Oceania, provided a figure of the type (P1. IV, C) which is

[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

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housed in the BPBM (3398). Measurements of the 106.8 mm SL male holotype (Fowler gave an undefined length of 134 mm) expressed as percent of standard length are given in Table 1. We obtained the following counts on this specimen: dorsal rays 86; anal rays 62; caudal rays 16; pectoral rays (both sides) 12; lateral-line scale rows 130; pored lateral-line scales 83; gill rakers 19 (5 + 14). Fowler (1923) gave counts of 132 scale rows and 20 gill rakers (6 + 14). Otherwise, our counts agree with his.

Photographs of recently collected female (106.4 mm SL) and male (114.4 mm SL) specimens (both BPBM 14102) are shown in Figures 1 and 2.

Counts

Dorsal and anal ray counts, expressed as bivariate relations, for 101 specimens are given in Table 2. Dorsal rays ranged from 84 to 95 ($\bar{X}$ = 87.9) and anal rays ranged from 64 to 70 ($\bar{X}$ = 66.3). Although the dorsal ray counts are skewed to the right, the distribution does not deviate significantly from a normal distribution ($P>0.2$; Kolomogorov-Smirnov test for goodness of fit, D = 0.0702).

There were considerably fewer pored lateral-line scales (Table 3) ($\bar{X}$ = 80.9) than the number of vertical scale rows above the lateral line ($\bar{X}$ = 131.6).

There was a tendency towards more pectoral rays (Table 3) on the ocular side ($\bar{X}$ = 12.24) than on the blind side ($\bar{X}$ = 11.49). The upper pectoral ray on the ocular side is reduced and sometimes inconspicuous. The upper pectoral ray on the blind side is also reduced, but easily visible.

Bothus thompsoni appears to be unique among species of *Bothus* in usually possessing 16 caudal rays. Of 163 specimens examined (Table 3), 2 (1.2%) had 15 rays, 157 (96.3%) had 16 rays, and 4 (2.5%) had 17 rays. The caudal rays are usually associated with the four hypural elements. Of 31 cleared and stained specimens having 16 rays, 11 had a caudal ray formula of 4-4-4-4 (dorsal element counted first). Other formulae obtained and number of specimens are as follows (rays articulating between elements are enclosed by parentheses): 4-4-3-(1)-4, (6 specimens); 4-4-3-5, (5 specimens); 3-(1)-4-4-4, (4 specimens); 3-(1)-4-3-(1)-4, (2 specimens); 3-(1)-4-3-5, (1 specimen); 3-(1)-4-3-5, (1 specimen); 4-4-3-5, (1 specimen). Two specimens with 15 rays had formulae of 4-4-3-4 and 3-(1)-4-4-3.

None of the caudal rays of *B. thompsoni* was associated with the neural and haemal spines of the penultimate vertebra or articulated in the space between the spines and hypural elements. Thus, *B. thompsoni* differs from certain other species of *Bothus* which have rays associated with the neural and haemal spines of the penultimate vertebra or which occur in the interspace between the spines and hypural elements. Gutherz (1970) gives a formula of 1-4-4-3-4-1 for larval *Bothus* (species not determined) from the western North Atlantic. We obtained the same formula for 12 cleared and stained specimens of *B. pantherinus* (Rüppell) from the Hawaiian Islands. In these specimens the first and last rays most often articulated in the interspace between the spines and hypural elements. These

TABLE 1.—*Bothus thompsoni:* Measurements of 13 characters for holotype, 29 males, and 31 females expressed as percent of standard length. Holotype excluded from regression statistics (a = ordinate intercept, b = regression coefficient).

Characters measured	Holotype BPBM 3398 percent of standard length	Range percent standard length for males	a	b	r^2	Range percent standard length for females	a	b	r^2
Head length	28.5	25.7-29.5	0.646	0.270	0.965	26.0-29.6	1.100	0.264	0.983
Snout length: to upper eye	23.9	14.0-21.5	−5.865	0.252	0.961	13.0-16.6	−1.022	0.162	0.968
to lower eye	6.3	4.4- 6.2	0.315	0.048	0.821	4.8- 6.8	−0.171	0.569	0.857
Orbit diameter: upper	11.6	9.1-12.6	2.255	0.084	0.828	8.2-12.4	1.656	0.087	0.896
lower	9.6	7.6-10.9	2.222	0.071	0.811	8.0-11.5	2.263	0.067	0.874
Interorbital distance	14.9	7.7-13.5	−5.856	0.182	0.958	5.1- 8.6	−1.112	0.088	0.949
Length of upper jaw	10.3	8.0-10.6	1.102	0.081	0.856	8.2-10.4	0.770	0.084	0.943
Greatest body depth	60.8	57.7-66.0	−1.046	0.629	0.968	57.0-67.3	−0.057	0.632	0.973
Least depth caudal peduncle	11.2	9.7-11.4	0.042	0.107	0.970	9.2-11.6	0.195	0.104	0.981
Length of pectoral fin: ocular side	21.7	19.0-24.7	4.661	0.159	0.912	18.8-24.9	4.925	0.153	0.924
blind side	18.4	15.3-18.7	2.294	0.141	0.928	14.0-18.5	0.826	0.155	0.930
Length of anal fin base	75.2	73.4-77.4	2.373	0.734	0.958	71.9-84.8	−3.634	0.814	0.966
Snout to greatest body depth	46.3	41.6-48.6	−4.156	0.497	0.959	41.4-50.0	0.341	0.452	0.961

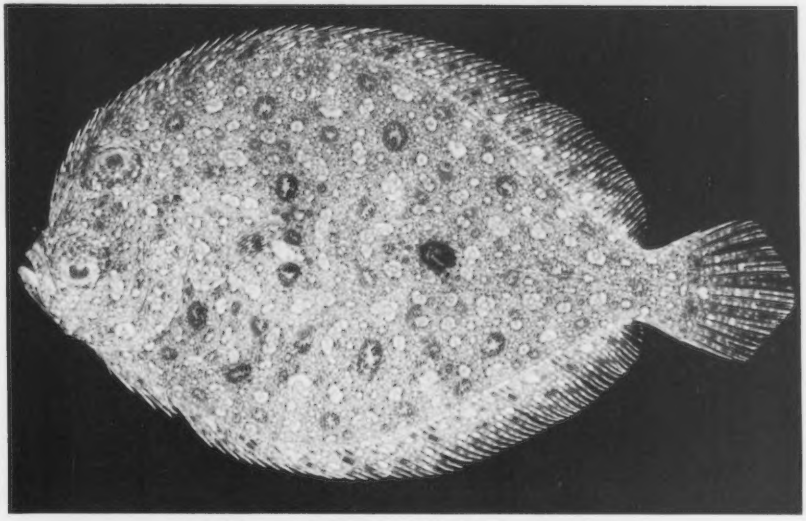

FIGURE 1.—A 106.4 mm SL female *Bothus thompsoni*.

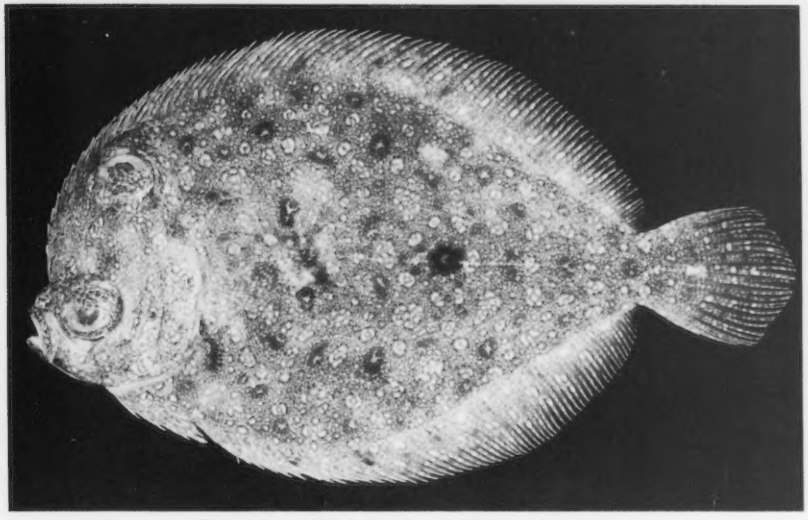

FIGURE 2.—A 114.4 mm SL male *Bothus thompsoni*.

data indicate that *B. thompsoni* exhibits a more variable caudal ray formula than *B. pantherinus*.

The first two and last two caudal rays of *B. thompsoni* are usually simple. Of a sample of 20 specimens, only 2 (10%) had either the second or penultimate ray divided.

The arrangement of gill rakers in *B. thompsoni* is shown in Figure 3, and counts are given in Table 3. There are 3-9 reduced gill rakers associated with the epibranchial and 1-4 reduced gill rakers associated with the hypobranchial. A series of 9-14 well-developed gill rakers is principally associated with the ceratobranchial. The reduced gill rakers associated with the epibranchial comprise the counts for the upper limb of the gill arch. The first well-developed

TABLE 2.—Dorsal and anal ray counts for 101 specimens of *Bothus thompsoni*.

Number of anal rays	Number of dorsal rays												Total number of specimens
	84	85	86	87	88	89	90	91	92	93	94	95	
70	—	—	—	—	—	—	1	—	—	—	—	1	2
69	—	—	—	—	—	1	—	1	—	—	—	—	2
68	—	—	—	—	1	3	1	4	1	—	—	—	10
67	—	—	2	5	7	7	5	3	1	—	—	—	30
66	—	3	7	3	9	8	—	—	—	—	—	—	30
65	2	—	8	7	3	—	—	—	—	—	—	—	20
64	2	1	2	1	1	—	—	—	—	—	—	—	7
Total number of specimens	4	4	19	16	21	19	7	8	2	—	—	1	101

raker occurs at the angle of the arch and is included in the counts for the lower limb, although stained material reveals this raker to be more closely associated with the epibranchial. The last one or two well-developed rakers are associated with the hypobranchial.

The number of gill rakers in the size range examined is apparently independent of size. A regression coefficient calculated for 28 females was not significant ($P > 0.4$).

Vertebral counts were obtained from 96 specimens. There are usually 10 abdominal vertebra (94 specimens), but two individuals had 11 (28 caudal vertebrae in both cases). Counts of caudal vertebrae (including urostyle) were 27 (7), 28 (69), and 29 (18), while total vertebral counts were 37 (7), 38 (69), and 39 (20).

FIGURE 3.—A typical first gill arch from the ocular side of *Bothus thompsoni*.

Measurements

The measurements obtained from 29 male and 31 female specimens for 13 characters are summarized in Table 1. Linear regressions were calculated in original units of measurement (mm) with standard length as the independent

TABLE 3.—*Bothus thompsoni*: Counts for eight characters.

Characters	Frequency of occurrence																					N	$\bar{X}$
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
Caudal rays	-	-	-	-	-	-	-	-	-	-	-	-	2	157	4	-	-	-	-	-	-	-	163	16.01
Pectoral rays (ocular side)	-	-	-	-	-	-	-	1	7	32	22	1	-	-	-	-	-	-	-	-	-	-	63	12.24
Pectoral rays (blind side)	-	-	-	-	-	-	-	2	29	31	1	-	-	-	-	-	-	-	-	-	-	-	63	11.49
Gill rakers (upper limb)	1	5	29	29	21	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	91	5.92
Gill rakers (lower limb)	-	-	-	-	-	-	-	-	1	3	21	22	27	13	4	-	-	-	-	-	-	-	91	14.38
Gill rakers (total)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	11	13	24	9	17	6	5	91	20.30

	70-71	72-73	74-75	76	78	80	82	84	86	88	90-91	92-93											
Pored lateral line scales	1	-	-	5	6	8	3	4	2	1	-	1										31	80.9

	114-115	116-117	118-119	120-121	122-123	124	126	128	130	132	134	136	138	140	142	144	146-147						
Lateral line scale rows	1	-	-	-	4	2	6	6	17	5	6	8	5	-	1	-	2					63	131.6

variable. Plots of all regressions are linear and exhibit high r^2 values.

The regressions obtained for the 13 measured characters were subjected to analysis of covariance to test for sexual dimorphism. Highly significant differences ($P<0.001$) were found between the regression coefficients for two characters (which are related): interorbital distance (Figure 4) and snout to upper eye. Juvenile and adult male specimens of *B. thompsoni* are similar to many *Bothus* spp. males in possessing a much greater interorbital distance than females of the same species. Male *B. thompsoni* exhibit positive allometric growth of the interorbital distance, this measurement being about 7.5% - 9.0% of standard length at a length of 50-60 mm and about 12% -14% of standard length at a length of 100-115 mm. In female specimens longer than 50 mm the interorbital distances were 6.0% - 8.6% of standard length. Interorbital distances of 5.3% and 5.1% of standard length were noted in two specimens 39 mm and 48 mm long. As expected, male *B. thompsoni* exhibited positive allometric growth of the snout to upper eye distance.

Among the remaining 11 characters subjected to analysis of covariance, there were no significant differences between regression coefficients. There were significant differences ($P<0.05$) in the elevations of the regressions between sexes for four characters. Both the upper and lower orbit diameters of males tend to be larger than for females; the differences in adjusted means for the two characters are 0.35 and 0.40 mm, respectively. Females tend to have a greater body depth and a greater snout to greatest body depth distance. The differences in adjusted means for these two characters are 1.1 and 1.0 mm, respectively.

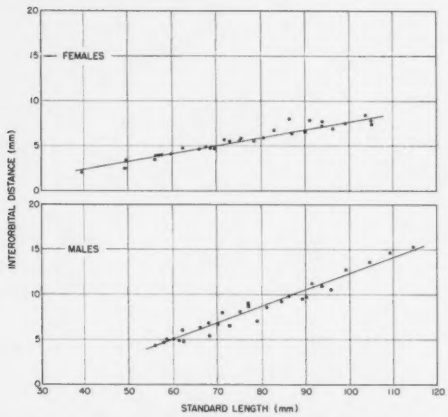

FIGURE 4.—Plots of the interorbital distance of 29 male and 31 female specimens of *Bothus thompsoni*.

In both sexes, the pectoral fins of the ocular side tend to be longer than those of the blind side (Table 1). The pectoral fins of both sexes exhibit negative allometric growth. This is most pronounced on the ocular size where the pectoral length is about 24% -25% of standard length at 40-60 mm and about 18% -21% of standard length at a length of 100-115 mm. There is only slight negative allometric growth of the pectoral fin on the blind side where this structure varies from 14.0% to 18.7% of standard length.

All other morphometric characters examined exhibited approximately isometric growth.

Two of the measurements we obtained for the holotype (Table 1) do not fall within the ranges we obtained from our study series: interorbital distance and snout to upper eye.

Other morphological characters

Bothus thompsoni has cycloid scales on the blind side and on most of the ocular side (Figure 5A). Ctenoid scales occur on the proximal portions of the dorsal and anal rays. There are 2-3 rows of ctenoid scales at the bases of the dorsal and anal fins (Figure 5B). Fowler (1923) stated that the holotype had ctenoid scales on the cheeks and postorbital region. In addition, we find that there is a patch of about 15 ctenoid scales below the curved portion of the lateral line in the holotype. A scale from this region is shown in Figure 5C. The occurrence of ctenoid scales on the cheek and in the vicinity of the curved portion of the lateral line is a variable character. Of 25 specimens (67.5-106.4 mm SL) from our study series, six had ctenoid cheek scales, three had ctenoid scales on the cheek and near the lateral line, and one had ctenoid scales near the lateral line only. The presence of ctenoid scales in these two regions does not appear to be related to size or sex. The cycloid scales are small and nonimbricated, but the ctenoid scales at the dorsal and anal fin bases overlap to a slight degree. The ctenii of the ctenoid scales generally occur in two rows: a primary row of well-developed ctenii and a secondary row of smaller ctenii basal to the

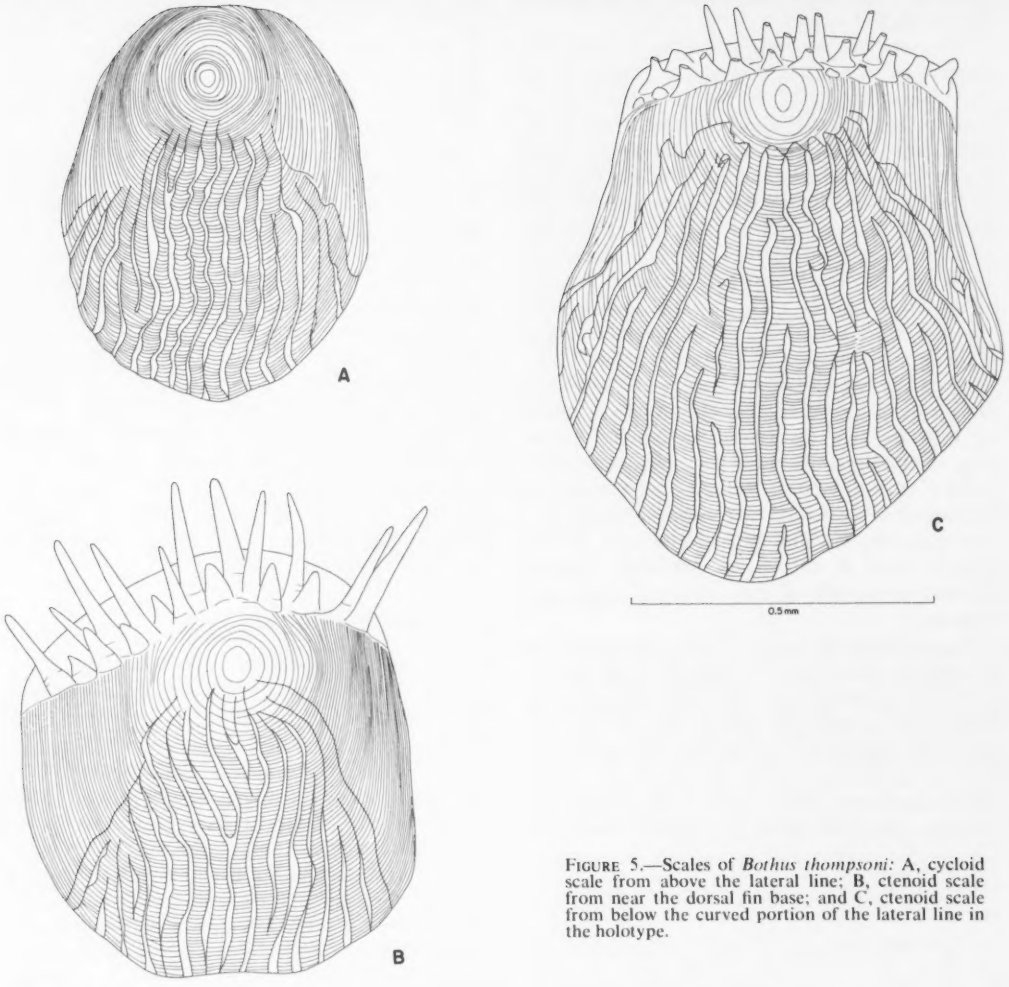

FIGURE 5.—Scales of *Bothus thompsoni:* A, cycloid scale from above the lateral line; B, ctenoid scale from near the dorsal fin base; and C, ctenoid scale from below the curved portion of the lateral line in the holotype.

primary row (Figure 5B and C). The number of ctenii on cheek scales varies from 5 to 8, while scales from the dorsal and anal fin bases at the greatest body depth have 15 to 25 ctenii.

The general arrangement of teeth in the upper and lower jaws is shown in Figure 6. There are usually three rows of teeth. The outer row consists of a few, stout conical teeth in the anterior portion of the jaws. The middle row consists of more numerous, but less stout, conical teeth. The inner row consists of depressed, poorly ossified conical teeth subequal in number to those in the middle row (except on the blind side of the upper jaw). The inner row of teeth are movable, being held in place by flesh and not inserted in the jaw bones.

The number of outer teeth, and, to a lesser extent, the middle teeth, vary according to jaw bone and size of specimen. This is illustrated in Figure 7 where the number of teeth are plotted by standard length for 10 females 49.2-106.4 mm SL and 10 males 55.8-114.5 mm SL. The increase in number of outer teeth with size is apparent for all jaw bones except the dentary on the ocular side. There also appear to be more outer teeth in the premaxillary of the ocular side of the males.

The teeth in the middle row also exhibit a general, but less well-defined, increase in numbers with size.

There are no fleshy papillae along the edges of the eyes such as reported for male *B. pantherinus* (Norman, 1934). There is a single prominent, blunt protuberance on the snout of males greater than 60 mm SL. This structure is represented in females by a small knob. The anterior edge of the lower orbit tends to be more developed and rugose in males than in females.

Coloration of fresh specimens

The blind side of both sexes is white, but tending to dusky white in males greater than about 80 mm SL, especially on the cheek and above the cheek. The ground color of the ocular side is light olive green. There is a single prominent dark spot on the lateral line posteriad about 60% of the standard length. There are two secondary dark ocelli near the pectoral fin. There are 14-15 olive green ocelli broadly distributed along the dorsal and ventral borders of the trunk. There are numerous light blue ocelli and spots distributed over the trunk, head, and dorsal, anal, caudal, and ventral fins. The pectoral fins are almost clear. In males, the light blue spots are more numerous and elongated along the anterior profile and between the eyes.

Comparison with Other Species of *Bothus*

A definitive discussion of the relation of *B. thompsoni* to other species of *Bothus* must await further study of the genus on a worldwide basis. *B. thompsoni* differs from all recognized species of *Bothus* (Fowler, 1933; Norman, 1934; Chabanaud, 1942; Stauch, 1966; Gutherz, 1967; Amaoka, 1969; Topp and Hoff, 1972) in possessing 11-17 gill rakers on the lower limb of the first arch (11 or fewer in other species) and 115-147 scale rows above the lateral line (apparently 100 or fewer in other species: Norman, 1934). It may also be unique in that it usually has only 16 caudal rays as opposed to 17 in other species. This character, however, apparently has been examined only rarely by earlier authors and few data on the numbers and arrangements of the caudal rays are available (Chabanaud, 1942; Amaoka, 1969; Gutherz, 1970). The figures given by Norman (1934) for *B. leopardinus* (Günther) and *B. bleekeri* indicate

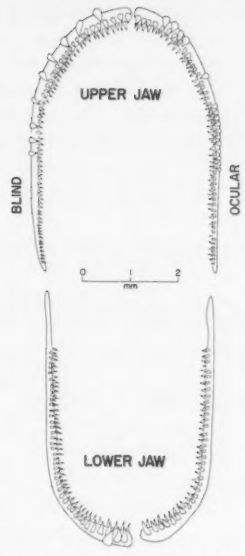

FIGURE 6.—The arrangement of teeth in *Bothus thompsoni*.

caudal ray counts of 16. However, a count of 16 is also indicated for *B. ovalis* (Regan) which Amaoka (1964) has shown to be the young of *B. myriaster* (Temminck and Schlegel). *B. myriaster* has 17 caudal rays (Amaoka, 1969). Chabanaud (1942) described *B. budkeri* from the Red Sea and gave caudal ray counts of 16 for the holotype and 17 for the two paratypes. A sample of 368 adult and larval specimens of *B. pantherinus* from the Hawaiian Islands had the following caudal ray counts: 16 (2.7%), 17 (95.7%), 18 (1.6%). Further examination of this character is required.

We have not examined specimens of *B. bleekeri*, and we separate this species from *B. thompsoni* on the basis of the description given by Norman (1934). In addition to the differences in gill raker and lateral line scale row counts discussed above, *B. thompsoni* has more pectoral rays on the ocular side (10-14 vs. 8-9). Adult male specimens of *B. thompsoni* do not have elongated pectoral rays (ocular side), whereas male *B. bleekeri* have elongated pectoral rays.

Two other species of *Bothus*, *B. pantherinus* and *B. mancus* (Broussonet), occur in the Hawaiian Islands. Adult specimens of *B. thompsoni* may be separated from similar life history stages of the former two species on the basis of body profile alone. Other useful characters for

distinguishing *B. thompsoni* from *B. pantherinus* and *B. mancus* (in addition to counts of the lateral line scale rows, lower gill rakers, and caudal rays) are as follows. Cycloid scales are present on the ocular side of *B. thompsoni* (except at the bases of the dorsal and anal fin, and occasionally on the cheeks and in the vicinity of the lateral line) as opposed to ctenoid scales on the ocular side for *B. pantherinus* and *B. mancus*. Adult males of the latter two species have elongated pectoral fin rays on the ocular side, while male specimens of *B. thompsoni* do not. *Bothus mancus* possess more dorsal and anal fin rays than do *B. thompsoni* and *B. pantherinus* (97-102 vs. 84-96 and 77-82 vs. 64-74, respectively; Hawaiian Island

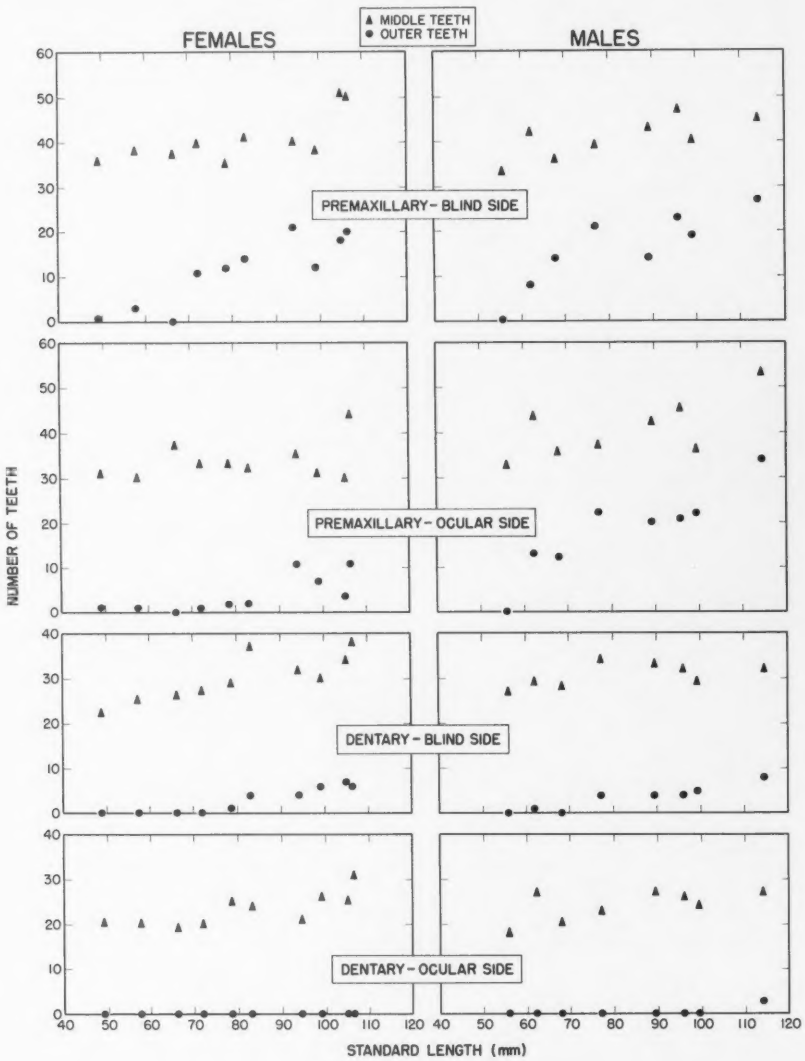

FIGURE 7.—Numbers of teeth in the outer and middle tooth rows in *Bothus thompsoni*.

specimens). *Bothus thompsoni* has 10-14 pectoral rays, whereas this count is 9-11 for both *B. pantherinus* and *B. mancus*.

With regard to other Indo-Pacific species recognized by Norman (1934), *B. thompsoni* differs from *B. myriaster* in that the pectoral fins of males are not elongated in the former species. The combination of cycloid and ctenoid scales on the ocular side of *B. thompsoni* differentiates it from *B. assimilis* (Günther) which has only cycloid scales and from *B. leopardinus* (Günther) which has only ctenoid scales on the ocular side (Norman, 1934). Norman (1934) considers also that *B. constellatus* (Jordan, *in* Jordan and Goss) is very doubtfully distinct from *B. leopardinus*.

Although no illustration was given of *B. budkeri* (Chabanaud, 1942) from the Red Sea, it differs from *B. thompsoni* in having a lesser body depth, fewer dorsal and anal rays, fewer gill rakers on the lower limb of the first arch, and only ctenoid scales on the ocular side.

Fowler (1933) described five species of *Bothus* from the Philippines and China Sea. The generic placement of several of these species is questionable. At any rate, none of them could be confused with *B. thompsoni*.

Ecology

With the exception of one specimen caught at a depth of 72 m off Maui, all specimens of *B. thompsoni* taken to date have come from depths of 90-113 m off the north coast of Oahu where bottom temperatures ranged from 24.5° to 26.0°C. About 580 specimens (32-107 mm SL) have been obtained at 13 stations where catches ranged up to 275 individuals per haul. An analysis of dispersion for this species (Struhsaker, 1973) shows it to have a highly clumped distribution. The type of bottom in the area of capture is primarily muddy sand interspersed with patches of sponge, broken shell, and rubble. *Bothus thompsoni* was often taken with 20-30 other species of fishes; it usually comprised less than 8% of the total catch, but occasionally ranged up to 30%. Numerically dominant species taken with *B. thompsoni* include *Trachinocephalus myops*, *Priacanthus* spp., *Antigonia eos*, *Parupeneus chrysonemus*, and *Lagocephalus hypselogeneion*. Struhsaker and Higgins (manuscr.[2]) have shown that *B. thompsoni* is the third most abundant larval flatfish (after *Engyprosopon xenandrus* Gilbert and *B. pantherinus)* taken in offshore midwater hauls near Oahu. They also presented evidence that *B. thompsoni* may spawn throughout the year.

ACKNOWLEDGMENTS

We thank John E. Randall for the photographs used in Figures 1 and 2 and for reviewing the manuscript. We are also indebted to Elbert H. Ahlstrom and C. Richard Robins for comments on the manuscript. The NMFS Systematics Laboratory provided the radiographs. The illustrations are by Tamotsu Nakata and Robert Bonifacio.

MATERIAL EXAMINED

USNM 208494: TC-33-52 (R/V *Townsend Cromwell*, cruise 33, station 52); 1 male (109.2 mm SL); lat. 19°58.3′ N, long. 156°28.5′ W; depth 72 m, 13 Nov. 1967. USNM 208495: TC-36-15; 4 females (93.7-99.1 mm SL); lat. 21°37.7′ N, long. 158°08.8′ W; depth 113 m, 2 May 1968. USNM 208496: TC-36-20; 7 females (39.5-72.8 mm SL), 12 males (55.8-81.2 mm SL); lat. 21°36.8′ N, long. 158°12.5′ W; depth 110 m, 3 May 1968. USNM 208497: TC-40-115; 10 females (56.9-87.3 mm SL), 5 males (70.0-84.5 mm SL); lat. 21°36.8′ N, long. 158°08.2′ W; depth 102 m, 8 Nov. 1968. USNM 208498: TC-40-116; 4 females (56.0-105.4 mm SL), 3 males (58.6-104.5 mm SL); lat. 21°36.8′ N, long. 158°11.6′ W; depth 112 m, 1 Dec. 1968. USNM 208499: TC-40-119; 5 females (78.6-91.2 mm SL), 7 males (86.2-99.2 mm SL); lat. 21°36.8′ N, long. 158°11.2′ W; depth 96 m, 1 Dec. 1968. BPBM 14102: TC-40-125; 1 female (106.4 mm SL), 1 male (114.4 mm SL); lat. 21°36.8′ N, long. 158°11.6′ W; depth 102 m, 10 Nov. 1968.

[2] Struhsaker, P., and B. E. Higgins. Unpubl. manuscr. Post-larval flatfishes (Pisces:Pleuronectiformes): Observations on the identity and ecology of 11 Hawaiian species. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812.

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NOTE

DEVELOPMENT OF EGGS AND EMBRYOS OF THE SURF CLAM, *SPISULA SOLIDISSIMA*, IN SYNTHETIC SEAWATER

The eggs of the surf clam, *Spisula solidissima*, have been used extensively for investigations of egg structure and embryonic development of bivalves. Allen (1951) has pointed out the advantages of the use of surf clam eggs for research of this nature. These studies have been limited, however, to areas where natural seawater was readily available, due to the unsuitability of most synthetic seawaters for supporting the embryonic development of bivalves (David A. Nelson, NMFS, Milford, Connecticut and Gerald Zaroogian, Environmental Protection Agency Laboratory, West Kingston, Rhode Island, pers. comm.).

Experimental Observations

We recently reared *Spisula solidissima* embryos in a synthetic seawater formulation developed by Zaroogian, Pesch, and Morrison (1969) as a culture medium in which to rear oyster embryos. Our observations were made in salinities of 25 and 30 ‰ at 10°, 15°, and 20°C water temperatures. Within these ranges we found 20°C to be the optimum temperature for development, allowing us to rear eggs to the 5-day-old stage (early veliger) with almost 100% survival and no signs of larval abnormalities. At 20°C polar body formation occurs in about 45 min and the two-cell stage in about 90 min. The early veliger, or straight-hinge stage, is reached in less than 24 h. At 15°C all stages of development are normal but somewhat delayed, with development to the straight-hinge stage requiring more than 24 h. At 10°C the rate of development of all stages is greatly retarded and many abnormal embryos are present. The majority of fertilized eggs held at 10°C requires more than 96 h to develop to the straight-hinge stage.

At 20°C we found that development of fertilized eggs in synthetic seawater was comparable to the best development observed in natural seawater.

This study did not involve testing embryonic development of *S. solidissima* in synthetic seawater over a wide range of salinities, but was limited to those salinities currently in use in other research programs within this laboratory. It appeared that there was no difference in survival and development of eggs to the 5-day-old stage at salinities of 25 and 30 ‰, the only salinities tested. In earlier work, however, Stickney (in Yancey and Welch, 1968) reported that *S. solidissima* eggs failed to develop under experimental conditions in salinities of less than 23 ‰ in natural seawater.

Since the synthetic seawater formulation developed by Zaroogian, Pesch, and Morrison (1969) can be readily prepared, its general acceptance could lead to a wider utilization of surf clam eggs by embryologists and cytologists with standardization of techniques and comparability of results not always possible when natural seawaters from different locations are used.

LaRoche, Eisler, and Tarzwell (1970), in studies of bioassay procedures for oil and oil dispersant toxicity evaluation, suggested the use of Zaroogian's seawater as a standard testing medium in place of natural seawater, the composition of which varies, especially in regard to the presence of trace metals, dissolved organics, and particulate matter. They recommended the use of Zaroogian's seawater because of its ability to support spawning adults and larvae of the American oyster, *Crassostrea virginica*, for at least 48 h without visible adverse effects, and adult mummichog, *Fundulus heteroclitus*, grass shrimp, *Palaemonetes vulgaris*, and sandworm, *Nereis virens*, for extended periods. Thus, when sufficient research has been performed in this area, it may be possible not only to hold adult animals but also to rear the eggs and larvae of these animals in the same synthetic seawater. This would be an obvious advantage in assessing comparative tolerances to pollutants of different life stages.

Collection and Maintenance of Surf Clams in the Laboratory

Although some information on the collection and maintenance of surf clams in the laboratory and their reproductive cycle has been published (Loosanoff and Davis, 1963; Ropes, 1968; Yancey and Welch, 1968), we feel it pertinent to this paper that it be reviewed and our own observations added.

Adult surf clams can be purchased from biological supply houses or collected in their natural habitat. The range of *S. solidissima* is along the Atlantic Coast of North America, from the Gulf of St. Lawrence to Cape Hatteras (Yancey and Welch, 1968). South of Cape Hatteras the surf clam is represented by *Spisula solidissima raveneli*, similar to *S. solidissima* but a smaller species. *S. solidissima* is found in sandy bottoms from the low-tide line to depths of 500 ft in waters of oceanic salinity. They are present in shallow water beds, at various points along their range, and are easily hand-gathered along the coasts of Delaware, New Jersey, Long Island (New York), Rhode Island, and Massachusetts. Our collections have come mainly from Little Narragansett Bay and the area of Point Judith, in Rhode Island.

Surf clams can also be obtained from commercial clam boats working the beds, but our observations have shown that hand-gathered clams are more suitable for laboratory purposes; those obtained from commercial sources are often damaged by the action of the hydraulic dredge used in harvesting. They suffer high mortalities soon after introduction into the laboratory and long-term survival of those remaining also seems inferior to that of hand-gathered stocks.

We feel that the best working size for laboratory animals to be used as a source of gametes is 4 to 5 inches. Larger ones require more space and do not survive as well in crowded tanks. Smaller animals are more difficult to spawn, even though we have found some specimens as small as 5 cm to have viable sex products.

Ropes (1968), in a study of the reproductive cycle of offshore surf clam populations, found a biannual cycle during 3 years of the 4-year period covered by his study. This biannual cycle was characterized by a major mid-year spawning and a minor late-year spawning. He found ripe clams as early as May and as late as October during 3 years of the study. This pattern of ripeness may vary between inshore and offshore populations, depending on local temperature conditions. We found ripe clams only from June to August in inshore Rhode Island waters.

Surf clams can be collected prior to their natural spawning period and conditioned to ripeness in the laboratory. Conditioning refers to a procedure of gradually raising the water temperatures at which bivalves are maintained as a means of achieving gonad ripeness prior to the time one would expect to find ripe animals in the field (Loosanoff, 1954).

We have collected animals with unripe gametes from early winter through late spring (December to May) and conditioned them at 15°C. This temperature equals or exceeds that at which gametogenesis takes place in natural populations (Ropes, 1968). Such animals collected in early winter and conditioned in the laboratory have been spawned as early as March.

Ripe surf clams held in the laboratory at 15°C have never spawned spontaneously; thus, the spawning threshold of this animal in the laboratory would appear to be higher than 15°C. We do feel, however, even though we, as yet, lack quantitative data to substantiate it, that ripe animals held at 15°C tend to resorb their gametes more quickly than those held at a lower temperature following conditioning. Ripe animals collected in June and held at 10°C contained viable sex products in December.

Ropes (1968) reported that offshore populations spawn at lower temperatures than we found in our laboratory populations. He also noted that abrupt rises in water temperature were not clearly a cause of spawning in natural populations. A rapid increase in temperature is certainly an important factor in stimulating spawning in the laboratory. Clams conditioned at 15°C spawned when the temperature was raised quickly to 18-20°C. However, these clams were less responsive than those held in damp refrigeration (approximately 2°C, covered with a wet towel to prevent drying) overnight prior to exposure to 18-20°C. Refrigerated clams normally spawned within an hour after exposure to 18-20°C, while those conditioned at 15°C and exposed to water at 18-20°C did not.

Eggs and sperm can also be obtained by stripping the sex products from the gonads using a

method described by Costello et al. (1957). This involves removing one shell and gill, exposing the visceral mass, and slicing into the gonad which overlays the digestive glands and viscera. Care should be taken to avoid cutting into the underlying intestines and digestive glands, as the presence of body fluids in the cultures of eggs appears to be detrimental to embryonic development. The eggs and sperm are washed into separate collecting containers. Most of the tissue and debris collected along with the gametes can be removed by selective screening.

Stripped eggs tend to be more irregular in shape than naturally spawned eggs but soon become spherical. Previous investigators (Loosanoff and Davis, 1963) have reported the diameter of spawned mature eggs to average 56.5 μ. Our measurements of rounded stripped eggs from ripe clams have agreed with this.

To fertilize the eggs a small quantity of sperm suspension is added to the egg suspension and mixed by rapid stirring; care must be taken to add only a small quantity of sperm as *Spisula* eggs are quite susceptible to polyspermy at high sperm concentrations (Allen, 1951). Following fertilization the germinal vesicle breaks down and a thin membrane forms a short distance above the surface of the egg.

In conclusion we would like to point out that this is the first time to our knowledge that *Spisula solidissima* embryos have been reared in synthetic seawater, although they have been previously reared in the laboratory in natural seawater. Not all synthetic seawaters currently available are suitable for this purpose but that developed by Zaroogian, Pesch, and Morrison has consistently given us good results. We feel that the ability to rear these embryos in synthetic seawater will enhance the value of surf clam eggs and embryos in embryological and cytological research by offering a standardized rearing medium and a comparability of results not always possible when natural seawaters from different locations are used, as well as making possible the use of these organisms in bioassay procedures where the composition of the seawater must be known.

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ERRATUM

Fishery Bulletin, Vol. 71, No. 3

PAUL, A. J., AND HOWARD M. FEDER, "Growth, recruitment, and distribution of the littleneck clam, *Protothaca staminea*, in Galena Bay, Prince William Sound, Alaska," p. 665-677.

1) Page 665, left column, first paragraph. The last sentence should read:
"Feder and Paul (1973) and R. Nickeron (Alaska Department of Fish and Game, pers. comm.) suggested that a small clam fishery is feasible in Prince William Sound since paralytic shellfish poison (P.S.P.) does not seem to be a problem there, and many beaches with sizable populations of *P. staminea* and the butter clam, *Saxidomus giganteus*, occur in the area."

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